THE UNIVERSITY OF ALBERTA

THE EFFECTS OF VARIOUS MODES AND QUANTITIES OF CHRONIC PHYSICAL ACTIVITY ON FIBER COMPOSITION AND CROSS SECTIONAL AREA IN SELECTED DEVELOPING RAT MUSCLES

by

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DEDICATION

To Mom and Dad

ABSTRACT

The effects of two different modes and quantities of chronic physical activity (CPA) upon the fiber composition and cross sectional area of selected developing rat skeletal muscles were studied. Thirty-six male Wistar rats were divided into six groups: young control (YCON), age matched control (CON), exercised aerobic (EAER), exercised anaerobic (EANA), trained aerobic (TAER) and trained anaerobic (TANA). After a seventeen day progressive training program, the endurance animals (EAER and TAER) were running continuously for 5 minutes at 40 m/min, 15% grade while the sprint animals (EANA and TANA) were running 10 bouts of 15 seconds at 80 m/min interspersed with 30 second rest intervals, 15% grade. For the next ten weeks the exercised animals were run once per week while the trained animals ran twice a day, four days per week. During this time an overload effect was maintained in the trained animals by gradually increasing the distance run per activity session. A similarity in work output between the two modes of CPA was achieved by equating the total distance run per activity sessions. This was ensured by randomly pairing each animal in the EAER and TAER groups with an animal from the EANA and TANA groups respectively.

Significant alterations of body weight occurred with development and CPA. Both muscle weight and relative muscle weight demonstrated changes with development, but not CPA. The fiber type populations of the soleus (SOL) and vastus lateralis white (VW) muscles underwent developmental changes. Selective combinations of CPA mode and quantity preferentially affected the fiber type composition of SOL, VW, vastus lateralis red (VR), and medial gastrocnemius (medial

GAST) muscles. In the medial GAST, the cross sectional fiber area of all three fiber types was increased with normal growth and preferentially altered by various CPA conditions. The estimated proportional fiber type contribution to total muscle cross sectional area (EPTM) remained constant through development for all three fiber types in the medial GAST. In the TANA condition of CPA the EPTM of fast twitch - oxidative - glycolytic (FOG) fibers decreased while the fast twitch - glycolytic (FG) fibers showed a proportional increase. No alterations were noted in the EPTM of slow twitch - oxidative (SO) fibers under any of the CPA conditions. These findings demonstrate that selective combinations of CPA modes and quantities result in preferential cellular adaptations in developing skeletal muscles. The occurrence, direction and magnitude of these alterations is highly specific in different muscles and may either maintain or accentuate normal developmental patterns.

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INTRODUCTION

Exercise physiologists have recently begun to monitor alterations at the cellular level in mammalian skeletal muscle in an attempt to elucidate the mechanisms underlying its adaptability to physical activity. Numerous histochemical, biochemical, metabolic and ultrastructural adaptations to various physical activities have been shown through the use of human biopsies and animal models (Close, 1972; Gollnick and Hermansen, 1973; Holloszy, 1973; Goldberg et al., 1975).

The existence of three skeletal muscle fiber types has been demonstrated in many mammalian species (Barnard et al., 1971; Burke et al., 1971; Peter et al., 1972; Ariano et al., 1973, Edgerton et al., 1975; Prince et al., 1977). Qualitative histochemical staining procedures were used by Peter et al. (1972) to develop a classification system based upon the contractile speed and predominant energy producing pathway of the different muscle fibers. In this system, fibers are categorized as either fast twitch - oxidative - glycolytic (FOG), fast twitch - glycolytic (FG) or slow twitch - oxidative (SO). Delineation of fast from slow twitch muscle fibers is achieved through the assessment of alkaline stabile myofibrillar ATPase while the oxidative or glycolytic capability may be determined through the presence of reduced nicotinamide adenine dinucleotide (NADH) diophorase or α-glycerophosphate dehydrogenase (α-GPD) respectively. The inherent neural and metabolic characteristics allow individual motor units to be selectively recruited through varying intensities and durations of physical activity (Baldwin et al., 1973, 1975; Gollnick et al., 1973b, 1973c, 1974; Staudte et al., 1973).

This preferential recruitment dictates the contraction speed of the whole muscle (Barnard et al., 1970; Close, 1972) thereby regulating substrate utilization and the type of catabolic metabolism (Pernow and Saltin, 1971; Baldwin et al., 1973; Gollnick and Hermansen, 1973; Holloszy, 1973).

Ultimately, the functional capacity of the muscle is limited by its structural and/or metabolic protein components. In working skeletal muscle, energy production must at least equal energy expenditure if the level of physical activity is to be maintained (Wenger and Reed, 1976). Concomitantly, the mechanical forces generated by the skeletal muscle must be equal to or greater than the antagonistic resistance for the physical activity to continue. Adaptations to a chronic physical activity overload may therefore be achieved by increasing the energy producing capabilities (Wenger and Reed, 1976) and/or the structural protein components (Gordon, 1967; Jaweed et al., 1974) of the muscle.

The occurrence of metabolic adaptations in response to chronic physical activity is supported by biochemical alterations in substrate storage and utilization as well as the activities and concentrations of enzymes of intermediary metabolism. Increases in glycolytic enzymes (Saubert IV et al., 1973; Staudte et al., 1973; Thorstensson et al., 1975; Jobin, 1977) and glycogen storage and utilization (Bergstrom and Hultman, 1967; Baldwin et al., 1975a) have been noted with sprint exercise and training. Numerous investigations have shown that endurance programs lead to increased activities of selected oxidative enzymes (Barnard et al., 1970; Baldwin et al., 1972; Holloszy,

1973, 1975; Terjung et al., 1973; Hubbard et al., 1974; Benzi et al., 1975; Hickson et al., 1975) as well as carbohydrate and fatty acid storage and utilization (Baldwin et al., 1975; Holloszy, 1975). The functional significance of these metabolic adaptations is an enhanced energy production capability resulting in an increased work capacity.

These metabolic adaptations have been substantiated and localized through the use of histochemical techniques. Research has indicated that the adaptations seen with chronic physical activity may be fiber type specific. Involvement in endurance activities has been related to increased FOG fiber percentages with a proportional FG fiber decrement in guinea pigs (Barnard et al., 1970; Faulkner et al., 1971, 1972; Maxwell et al., 1973), rats (Kowalski et al., 1969; Wilkinson et al., 1976), the Lesser Bushbaby (Edgerton et al., 1972) and humans (Prince et al., 1976, 1977) when compared to age matched sedentary controls. No significant variations were found in the SO fiber population (Edgerton et al., 1969; Maxwell et al., 1973; Prince et al., 1976, 1977). Similar shifts in fiber population have been observed with sprint activity (Saubert IV et al., 1973; Wilkinson et al., 1976). Conversely, other researchers (Mackie, 1977; Wilkinson, 1977) have noted increases in the FG fiber population at the expense of FOG fibers after a chronic sprint program. However, other investigators have not found shifts in fiber types with either endurance (Fitts et al., 1973; Mackie, 1977) or sprint overloads (Fitts et al., 1973; Saubert IV et al., 1973; Thorstensson et al., 1975; Mackie, 1977). The reasons for the lack of change in these studies is unclear, however, it may be related to insufficient overload in the intensity, duration or frequency of physical activity, and/or age, species or type of muscle studied. The

variations of fiber type profiles occurring between different species and muscles is well documented (Gillespie et al., 1970; Ariano et al., 1973). The vastus laterialis red, vastus lateralis white and soleus muscles are composed of homogeneous FOG, FG and SO fiber population respectively, while the medial head of the gastrocnemius exemplifies a heterogeneous muscle fiber profile.

Skeletal muscle hypertrophy corroborates the existence of a structural protein adaptation. Evidence related to this adaptation has been measured at both the gross and microscopic levels. Generally, increases in muscle girths and mass have been shown in response to weight lifting activities (Gordon, 1967; Gordon et al., 1967b, Jaweed et al., 1974; Thorstensson et al., 1976) but not endurance or sprint conditioning (Gordon, 1967; Fitts et al., 1973; Staudte et al., 1973; Terjung, 1976; Jobin, 1977; Wilkinson, 1977) Significant increases in strength have been noted without attendant alterations in gross muscle parameters (Gordon, 1967; Penman, 1970; Thorstensson et al., 1976). It may be hypothesized that the discrepancy is due to the selective hypertrophy of muscle fibers. In accordance with this hypothesis, the measurement of cross sectional fiber areas has shown selective hypertrophy in response to various physical activities. While many discrepancies exist, endurance activity has usually been associated with SO and FOG fiber hypertrophy while FG fiber enlargement often resulted from sprint or weight lifting programs (Carrow et al., 1967; Gordon et al., 1967a, 1976b; Gollnick et al., 1973a; Thorstensson et al., 1975, 1976; Prince et al., 1976, 1977; Wilkinson, 1977). Contrarily, Faulkner et al. (1971, 1972) have associated decreases in fiber area with endurance activity. Biochemical analysis

of myofibrillar and saroplasmic protein content in skeletal muscle has not served to clarify the responses. Weight lifting and sprint activities produced increased (Jaweed et al., 1974; Wilkinson, 1977) while endurance activities have shown no alterations (Hubbard et al., 1974b) as well as large increases (Gordon et al., 1967a, 1967b) in these subcellular components.

The differentiation process associated with normal skeletal muscle development result in significant postnatal adaptations within neural and metabolic systems. Rodent skeletal muscle fibers at birth are homogeneously slower than those of the adult (Gutmann et al., 1973). Twitch times tend to increase until five weeks of age when the SO fibers stabilize (Brown, 1973) while the FOG and FG fibers continue to increase until maturity at approximately 15-to 17-weeks of age (Buller et al., 1960). These contractile events are accompanied by developmental alterations in the activities of myofibrillar ATPase (Gutmann et al., 1974), glycolytic enzymes (Bass et al., 1970; Mann and Salafsky, 1970), and oxidative enzymes (Bass et al., 1970; Maxwell et al., 1973). The metabolic adaptations to growth are mirrored by shifts in the muscle composition from FOG towards either FG or SO fibers depending upon the specific muscle involved (Faulkner et al., 1971; Maxwell et al., 1973; Wilkinson et al., 1976; Mackie, 1977). Recent research seems to indicate a maintenance of the youthful fiber mosaic occurs when chronic endurance or sprint activities are undertaken during this developmental period (Muller, 1974; Wilkinson et al., 1976; Mackie 1977; Wilkinson 1977).

The diversity of results recorded in the literature seems indicative of a specificity of adaptation, dependent upon the components

of the stimulus as well as the muscle fiber composition and its preferential recruitment pattern in that particular physical activity. Glycogen depletion patterns elicited by single bouts of activity support the contention that motor unit recruitment is reflective of the type and magnitude of chronic stimulation (Armstrong et al., 1974, 1977; Gillespie et al., 1974; Sullivan and Armstrong, 1978). Burke and Edgerton (1975) identified FOG, SO and finally FG fibers as the preferred recruitment sequence for low intensity activity in rodents while short sprint activity called upon FG, FOG and then SO fibers. Subsequently, Sullivan and Armstrong (1978) have suggested that a heirarchy of muscle involvement exists within groups of similarly functioning muscles. Their data on rats indicated a progressively greater utilization of the lower oxidative capacity fibers located in more peripheral muscles followed by the more peripheral areas of a muscle cross section with increasing running speed. It seems reasonable to expect muscle fiber adaptations to chronic physical activities to follow these recruitment patterns.

Since the quantity of the overload has varied when attempts have been made to study the differential effects of sprint or endurance training on developing muscle fiber types (Walker, 1966; Faulkner et al., 1971, 1972; Maxwell et al., 1973; Terjung, 1976; Wilkinson et al., 1976; Mackie, 1977), it is necessary to attempt to make the quantity of the overload uniform and vary the mode. Therefore, the purpose of this study was to attempt quantification of two different modes and quantities of chronic physical activity and evaluate their effects upon the fiber composition and cross sectional area of

selected developing rat skeletal muscles.

DEFINITION OF TERMS

CPA - Chronic Physical Activity - The regular and vigorous movement of the body over an extended period of time.

Mode - The type of CPA, in this study, endurance or sprint.

END - Endurance - In this study, continuous 5 to 9 minute runs at 40 m/min, 15% grade.

SPR - Sprint - In this study, 10 to 18 bouts of a 15 second run at 80 m/min interspersed with 30 second rest intervals, 15% grade.

Quantity - The total amount of CPA administered; in this study either exercised or trained and measured as the total distance run in meters.

EX - Exercised - In this study, groups of animals which ran 200m/ CPA session, once a week for ten weeks.

TR - Trained - In this study development is related to the natural growth pattern of skeletal muscle as observed in sedentary control animals between 7 and 20 weeks of age.

Hypertrophy - An increase in the size of a muscle or muscle fiber caused by increments in the number of size of its intracellular protein components.

Hyperplasia - An increase in the number of muscle fibers composing a skeletal muscle through the longitudinal splitting of muscle cells.

FOG - Refers to muscle fibers which exhibit fast twitch - oxidative -

glycolytic characteristics.

FG - Refers to muscle fibers which exhibit fast twitch - glycolytic characteristics.

SO - Refers to muscle fibers which exhibit slow twitch - oxidative characteristics.

EPTM - The estimated proportional contribution (%) of a muscle fiber type to the total cross sectional area of the muscle.

Sch^2 - Scheffe multiple means contrast.

METHODOLOGY

EXPERIMENTAL DESIGN

In order to study the effects of two modes and quantities of chronic physical activity (CPA) on developing skeletal muscle, six experimental groups were formed. Four groups were exposed to selected conditions of CPA while two groups remained as controls (Table I). The CON group served as an age-matched sedentary control for the CPA groups and when compared with the YCON group, demonstrated the normal developmental pattern of skeletal muscle between 7 and 20 weeks of age. The other four groups elucidated the effects of various chronic physical activities upon skeletal muscle. Post hoc procedures were enacted, when appropriate, to determine if either the quantity or mode of CPA was responsible for the observed results (Table II). Four skeletal muscles with distinctly diverse fiber propulations were used in this study - vastus lateralis red portion (VR), vastus lateralis white portion (VW), soleus (SOL) and the medial head of the gastrocnemius (medial GAST). The dependent variables listed below were chosen as indicative parameters of growth, fiber composition and hypertrophy.

1. Body Weight (g);
2. Muscle Weight (g);*
3. Muscle Weight/Body Weight;*
4. Fast Twitch - Oxidative - Glycolytic (FOG) Fiber Types (%);
5. Fast Twitch - Glycolytic (FG) Fiber Types (%);
6. Slow Twitch - Oxidative (SO) Fiber Types (%)
7. FOG Cross Sectional Fiber Areas (μ^2);*
8. FG Cross Sectional Fiber Areas (μ^2);*
9. SO Cross Sectional Fiber Areas (μ^2);*
10. FOG Estimated Percentage Contribution to Total Cross Sectional Area (EPTM) (%);*
11. FG EPTM (%);*
12. SO EPTM (%);*

TABLE I EXPERIMENTAL DESIGN

Animal Group	N	CPA Condition Mode - Quantity	Amount of CPA/Session Time (Sec)	Amount of CPA/Session Distance Run (m)	Number of CPA Sessions/Week	Number of Weeks of CPA	Age at Time of Sacrifice (Wks)
YCON - Young Control	6	Sedentary	0	0	0	0	7
CON - Age-Matched Control	6	Sedentary	0	0	0	0	20
EAER - Exercise Aerobic	6	Endurance - Exercise	300	200	1	10	20
EANA - Exercise Anaerobic	6	Sprint - Exercise	150	200	1	10	20
TAER - Trained Aerobic	6	Endurance - Trained	300	200	8	10	20
TANA - Trained Anaerobic	6	Sprint - Trained	150	200	8	10	20

Variables marked with an (*) were measured on the medial GAST muscle only.

TABLE II DESIGN FOR ANALYSIS OF CHRONIC PHYSICAL ACTIVITY (CPA) COMPONENTS

Classification of CPA Components		Scheffe Multiple Contrast for Post Hoc Analysis
MODE	ENDURANCE	[a](EAER + TAER) - 2(CON)
	SPRINT	(EANA + TANA) - 2(CON)
QUANTITY	EXERCISED	(EAER + EANA) - 2(YCON)
	TRAINED	(TAER + TANA) - 2(YCON)

[a] Examples of multiple contrasts used.

EXPERIMENTAL ANIMALS

Thirty-six male Wistar rats (Woodlyn Farm, Guelph Ontario) weighing 136.1± 2.1g (approximately 6 weeks old) were acquired, numbered and randomly assigned to one of six groups (Table I). The animals were housed in individual, self-cleaning cages which were sterilized weekly. Since the rat is nocturnal, the day-night cycle was reversed (dark 0600 to 1800 hours) to permit the animals to be exercised or trained during

their wakeful period. Food (Purina Rat Chow) and water were provided ad libitum and the room temperature was maintained at 21 $\pm$ 1°C. Papers were changed, cages rotated, food and water replenished, and each animal handled daily. After arrival, all animals were permitted one week of familiarization to the new laboratory conditions, experimenters, and the reversed day-night cycle. After every exercise or training session each animal was towelled dry and inspected for injury. Any animals which were injured or become ill were treated appropriately and, if necessary, isolated. Body weights were monitored at the end of the familiarization week and after two, five, ten and thirteen (sacrifice) weeks in the lab.

CHRONIC PHYSICAL ACTIVITY REGIMEN

The chronic physical activity regimen was conducted on a motor driven treadmill (Quinton Company) consisting of ten 9.5 x 48 cm compartments. A shock grid was located at the back of each compartment for motivational purposes. The initial stimulus of 40 volts AC was arbitrarily increased to 80 volts AC as the animals grew and adapted to the shock.

At the end of the familiarization week the animals in the endurance (EAER + TAER) and sprint (EANA + TANA) groups were placed on a seventeen day progressive training program until criterion levels were reached (Table XXXVI, Appendix D). In an attempt to equate the amount of work between the endurance and sprint groups the following criterion treadmill speeds and grades were used:

Endurance -- a continuous 5 minute run at 40 m/min, 15% grade.

Sprint -- 10 bouts of a 15 second run at 80 m/min interspersed with 30 second rest intervals, 15% grade, for a total work time of 2 min 30 sec.

In this manner, the total distance run by the two groups per activity session was equal (i.e. 200m).

The exercise (EAER + EANA) groups were then run at this criterion once a week (Wednesday; 0700 hours) for ten weeks. The trained (TAER + TANA) groups were run eight times per week (Monday, Tuesday, Thursday, Friday; 0700 and 1500 hours) for ten weeks. Originally, the trained groups were to run at the criterion level until sacrifice. It was determined during the study that the training protocol be altered progressively (Table XXXVII, Appendix D) to maintain an overload effect. The final workloads attained were 9 minutes at 40 m/min, 15% grade for the TAER group and 18 bouts of 15 sec run/30 sec rest at 80 m/min, 15% grade for the TANA group. The CON animals were restricted to their cages throughout the study.

Each animal in the EAER and TAER groups was randomly paired with an animal from the EANA and TANA groups respectively. If an animal could not run due to illness or injury then the animal with which it was yoked was not run. This ensured that the total distance run by the matched groups was equated (Table IV, Appendix B).

After the twelfth week of training both the trained and exercised groups were subjected to a performance test to exhaustion approximately 72 hours prior to sacrifice (Table IV, Appendix B). For the performance test the aerobic animals were run continuously at 40 m/min and the anaerobic by 15 sec run/30 sec rest bouts at 80 m/min.

TISSUE COLLECTION, PREPARATION AND ANALYSIS

All animals were sacrificed by decapitation, quickly exsanguinated and the skin removed from the left hind leg. The gastrocnemius, soleus and vastus lateralis muscles were isolated, excised and freed of excess fat or connective tissue. The vastus lateralis muscle was divided into its red and white portions. The proximal one-third of each muscle was sectioned free, mounted in tragacanth gum on a cork and immediately frozen in liquid nitrogen cooled isopentane (2-methylbutane). The tissue was stored at -50°C for subsequent analysis. In the case of the gastrocnemius, only the medial head was used in the analysis while wet weights of the whole gastrocnemius were obtained from the contralateral limb (Table VI, Appendix B).

Transverse 10μ thick serial sections were cut on an American Optical Cryocut microtome at -22°C, mounted on microscope slides, and air dried. These serial sections were histochemically stained for myofibrillar ATPase (pH 9.4) according to the method of Padykula and Herman (1955) as modified by Guth and Samaha (1969), NADH-diaphorase according to Dubowitz and Brooke (1973) and α-glycerophosphate dehydrogenase (α-GPD) as suggested by Wattenberg and Leong (1960).

For each muscle an ATPase and NADH-diaphorase slide were simultaneously projected onto a white surface by two Bausch and Lomb Tri-Simplex microprojectors and identical areas of fibers were outlined. The fibers were then classified and counted according to the nomenclature of Peter _et al_. (1972) as described previously. The number of muscle fibers counted varied depending upon the muscle studied and the age of the animal (Table VII, Appendix B). Fiber

populations were expressed as a percentage of the total number of fibers counted.

Cross sectional muscle fiber areas were calculated for 30 fibers of each fiber type per cross section in the medial GAST using a digitizer. Color slides of ATPase stained sections were taken through a Shimadzu Kalnew No. 12680 microscope at a magnification of 70X using a 35 mm camera. To ensure accurate measurements a Bausch and Lomb Micrometer Disc (No. 31-16, 4 units = 1 mm) was photographed concurrently. These slides were then projected vertically at a magnification of 500X onto a Hewlett-Packard 9864A Digitizer integrated with a Hewlett-Packard 9825A Calculator. A calculator program (available upon request) based upon the trapezoidal rule (Riddle, 1970) was written and enabled the direct calculation of cross sectional area for each muscle fiber.

The proportional contribution of each fiber type to the total cross sectional area of the muscle was estimated by the following calculation:

$$\text{EPTM} = \frac{\%_f \cdot A_f}{\Sigma\,(\%f \cdot Af)} \cdot 100$$

where EPTM is the estimated proportion of the total muscle cross sectional area (%)

% is the mean percentage fiber population

A is the mean cross sectional area of a fiber type

and f is the fiber type (FOG, FG or SO).

STATISTICAL ANALYSIS

A one-way analysis of variance (ANOV15; Division of Educational Research Services) was used to compare the group means of the previously listed dependent variables. To locate significant differences between pairs of means a Scheffe multiple comparison of means post hoc procedure was used (Scheffe, 1964). Also, post hoc Scheffe multiple means contrasts (Glass and Stanley, 1970) were employed when appropriate to clarify the effects of the mode and/or quantity of chronic physical activity. In all cases, an alpha level equal to or less than 5 percent ($p \leq 0.05$) was required for the acceptance of a significant difference between means.

RESULTS

The results are presented under five major headings: Chronic Physical Activity Regimen, Body and Muscle Weights, Muscle Fiber Type Populations, Cross Sectional Fiber Areas, and Estimated Fiber Type Contributions. Group means and standard errors of the means (SEM) are graphed and/or tabulated. The raw data for all experimental animals are recorded in Tables IV through VIII, Appendix B. Summaries of the statistical analyses (Analysis of variance tables, Scheffe multiple comparison of means, probability matrices and Scheffe multiple means contrast tables) are contained in Appendix C, Tables XIV through XXXV.

CHRONIC PHYSICAL ACTIVITY REGIMEN

The total amount of chronic physical activity administered to the four experimental groups, expressed as the total distance run in meters (group mean), is displayed in Figure 1. There were no differences within the exercised or trained groups. The trained groups received significantly more (881.7%) chronic physical activity than the exercised groups (Table XIV, Appendix C).

The mean distance run by each of the four activity groups in the performance test is shown in Figure 2. The TANA group performed longer ($p<0.05$) than any of the other groups. When the data was pooled, significantly better performances were noted by the sprint and trained groups over the endurance and exercise groups respectively (Table XV, Appendix C). Complete data for each group on both of these parameters is contained in Table IV, Appendix B. It should

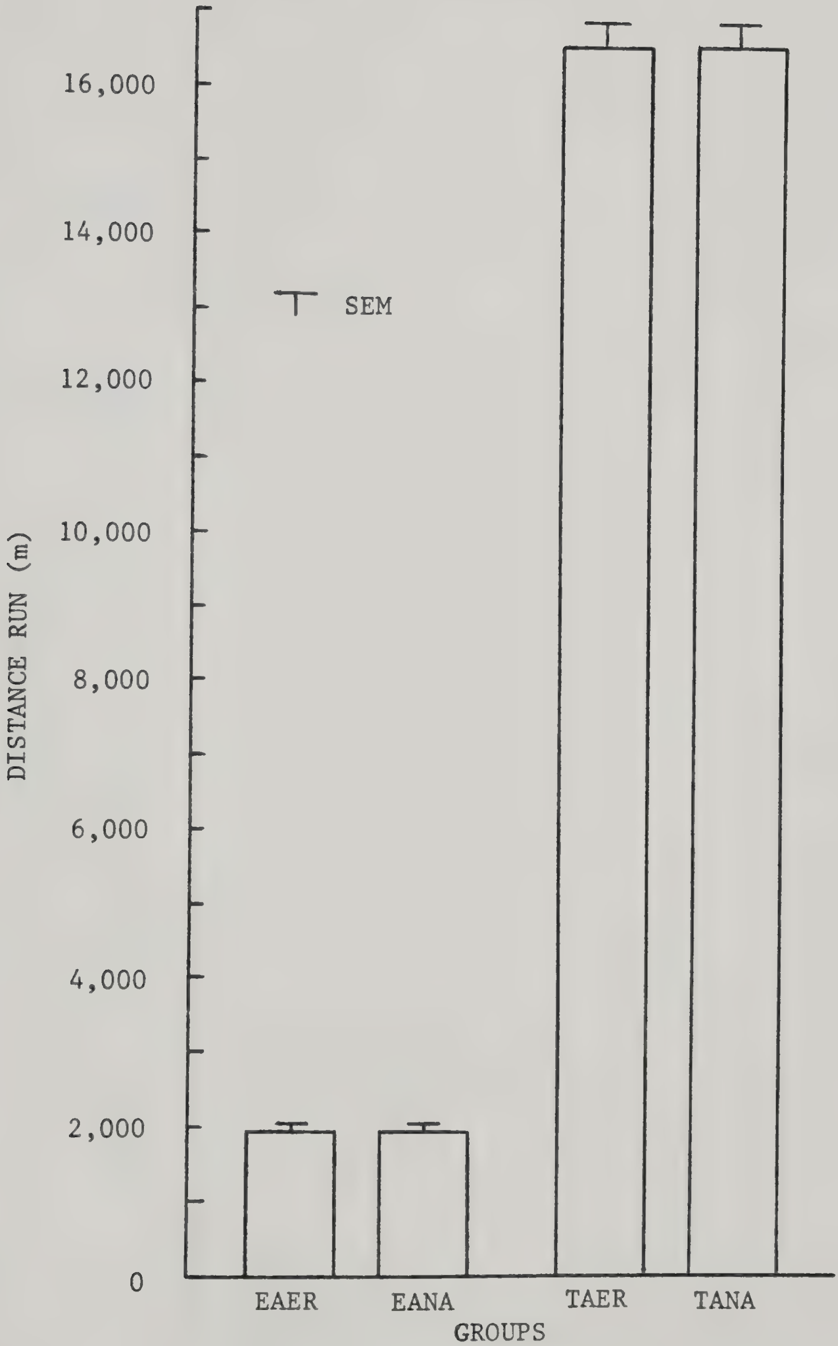

Figure 1: The total amount of chronic physical activity (CPA) administered to the four active groups (expressed as the mean total distance run in meters).

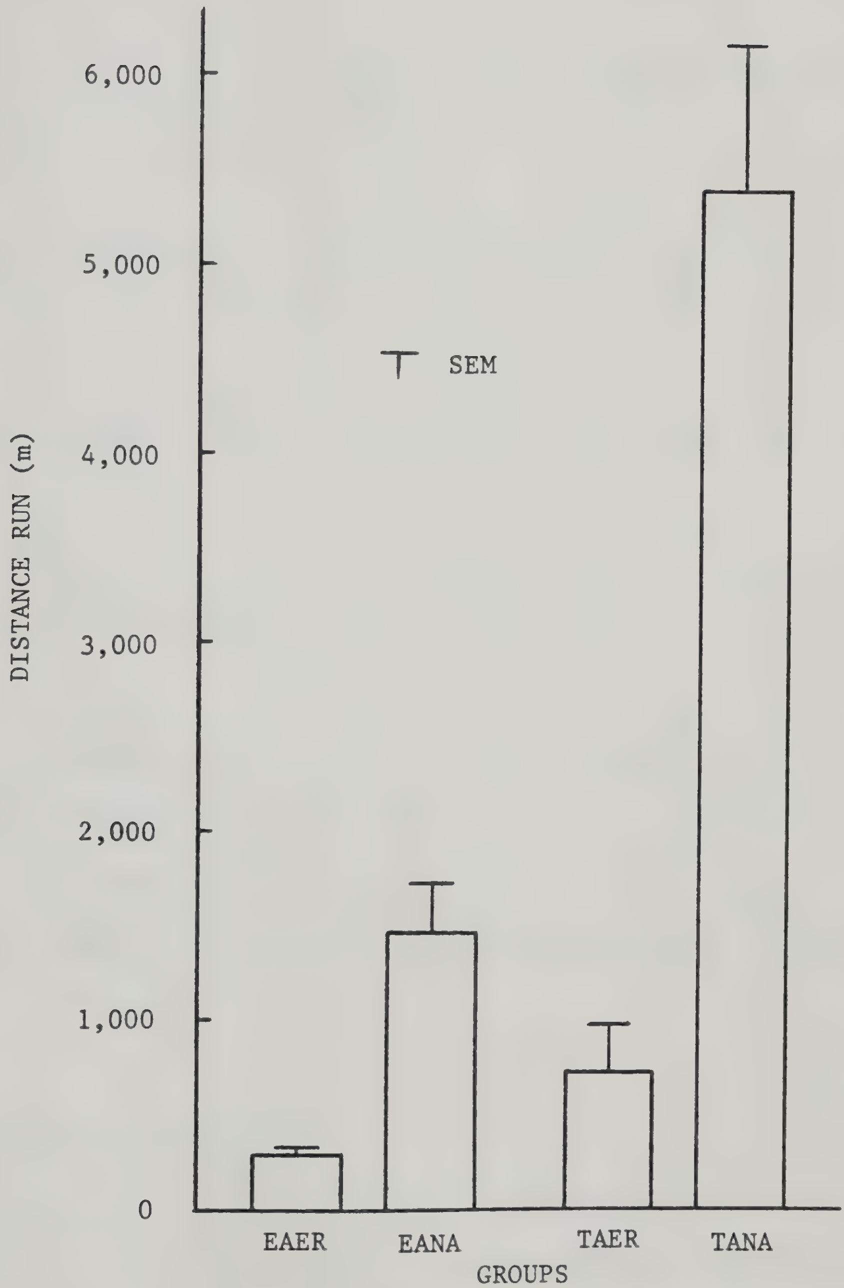

Figure 2: The mean distance run by the four active groups on a performance test conducted after 10 weeks of chronic physical activity (CPA).

be noted that no attrition occurred as a result of this chronic physical activity regimen.

BODY AND MUSCLE WEIGHTS

Table III contains the group means for body and muscle weights. No significant differences were noted in body weights at the onset of the experiment (Table XVI, Appendix C). After ten weeks of CPA only the TAER group displayed a body weight which was significantly lower than the CON group (Table XVII, Appendix C). In the two muscle weight parameters measured, wet whole gastrocnemius muscle weight and wet whole gastrocnemius weight x 10^3 divided by body weight, no significant differences were found between the physically active groups and age-matched controls (Tables XVIII and XIX, Appendix C). Significant developmental increases were seen in body weight and whole muscle weight (Tables XVII and XVIII, Appendix C). A significant decrease in the proportional contribution of the gastrocnemius muscle to total body weight occurred with development (Table XIX, Appendix C). None of these growth patterns were altered significantly by chronic physical activity. Complete data for body and muscle weights are located in Tables V and VI, Appendix B.

MUSCLE FIBER TYPE POPULATIONS

Complete data on the muscle fiber populations of the six animal groups for the four muscles studied may be found in Tables VII through XI, Appendix B. The statistical analyses are summarized in Tables XX through XXIX, Appendix C. The results are illustrated graphically in

TABLE III THE EFFECTS OF TIME AND CHRONIC PHYSICAL ACTIVITY (CPA) ON THE MEAN BODY WEIGHTS AND GASTROCNEMIUS MUSCLE WEIGHTS

VARIABLE	GROUPS					
	YCON	CON	EAER	EANA	TAER	TANA
Initial Body Weight (g)	[b]129.5 ± 4.0	133.2 ± 5.6	133.7 ± 4.9	138.7 ± 4.9	142.3 ± 5.9	139.3 ± 6.3
Body Weight at Sacrifice (g)	129.5[t] ± 4.0	416.5* ±17.1	386.2* ± 5.5	373.3* ±12.5	355.3*[t] ±13.8	384.5* ±10.7
Wet Gastrocnemius Muscle Weight (g)	0.629[t] ±0.04	1.704* ±0.08	1.552* ±0.05	1.554* ±0.04	1.454* ±0.08	1.487* ±0.05
Relationship[a]	4.84[t] ±0.21	4.10* ±0.15	4.03* ±0.16	4.16 ±0.16	4.08* ±0.08	3.86* ±0.06

[a]Values represent the ratio "muscle weight x 10^3/body weight"

[b]Values are group means ±SEM

* Significantly different from YCON ($p<0.05$)

t Significantly different from CON ($p<0.05$)

Figures 3 through 6. Chronic physical activity resulted in significant alterations of only FOG and FG populations in the VW and medial GAST muscles. In the medial gastrocnemius (Figure 6), the significant decrement in FOG fiber population and concomitant increase in FG was related to the TANA condition only (Tables XVII and XVIII, Appendix C). Further analysis revealed that the mode of CPA, in this case sprint, was related to this shift in fiber population. As shown in Figure 3, the adaptations which occurred in the VW were more dramatic. A progressive and significant shift in fiber populations toward FOG at the expense of FG was evidenced with increasing quantities of CPA irrespective of mode (Tables XX and XI, Appendix C). In both the vastus lateralis red and soleus muscles (Figures 4 and 5), no statistically significant alterations of fiber populations occurred (Tables XXII to XXVI, Appendix C). The SO fiber population did not change ($p<0.05$) in any of the four muscles regardless of the CPA stimulus administered.

Significant developmental adaptations occurred in the VW and SOL muscles (Tables XX, XXI and XXV, XXVI, Appendix C). As evidenced in Figures 3 and 5, development resulted in increased fiber populations of FG in the vastus lateralis white and SO in soleus. In both instances this shift was at the expense of a decreased FOG fiber population. This pattern was not altered by CPA in the soleus. The combined effects of CPA and development upon the VW fiber populations were complex. Significant alterations were observed with both the mode (endurance only) and quantity (exercise only) of CPA. In the VR muscle, the only alteration in the developmental pattern ($p<0.05$) was an increase in the FG fiber

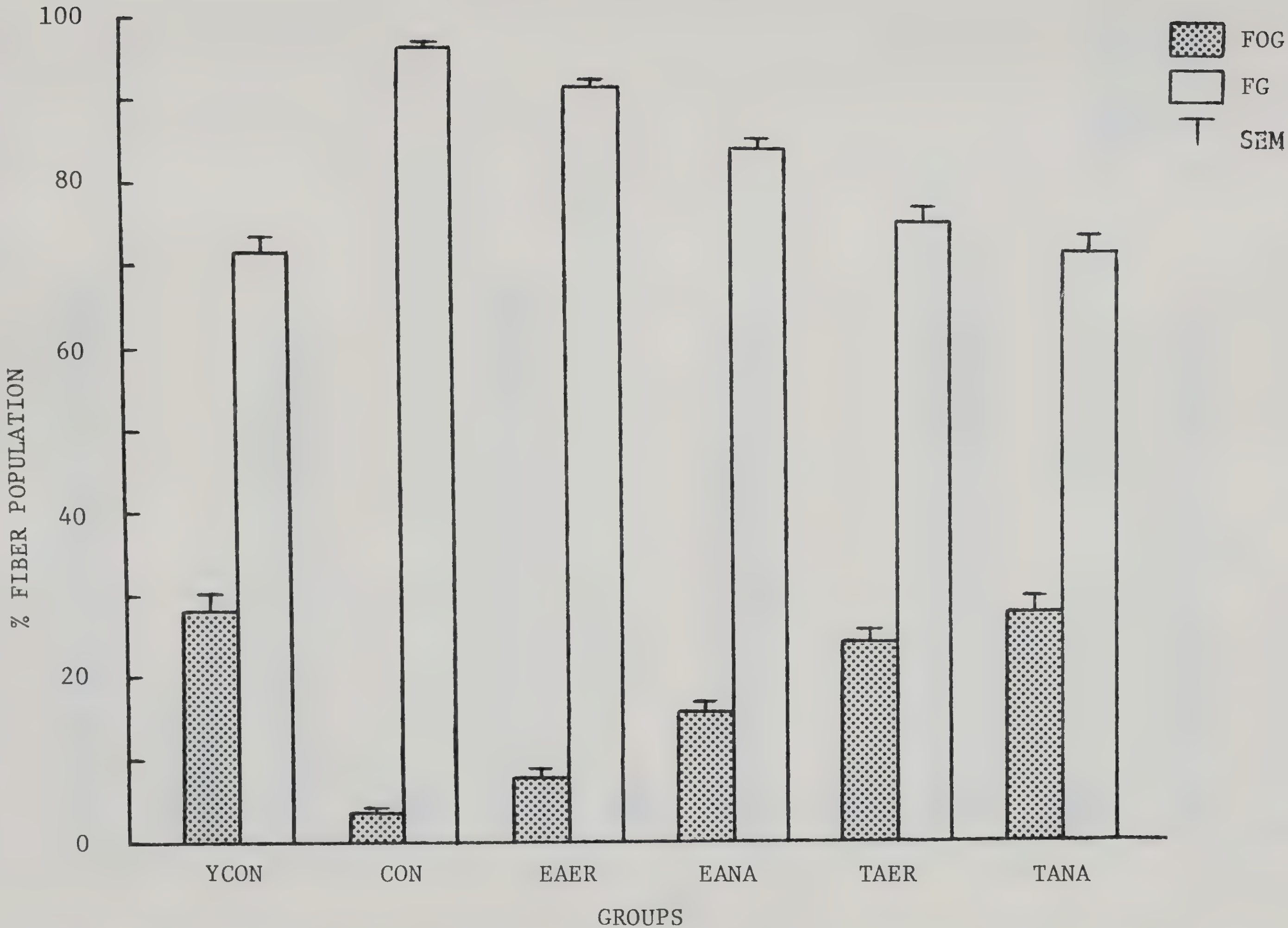

Figure 3: The effects of development and chronic physical activity (CPA) on the fiber type composition of the white vastus lateralis.

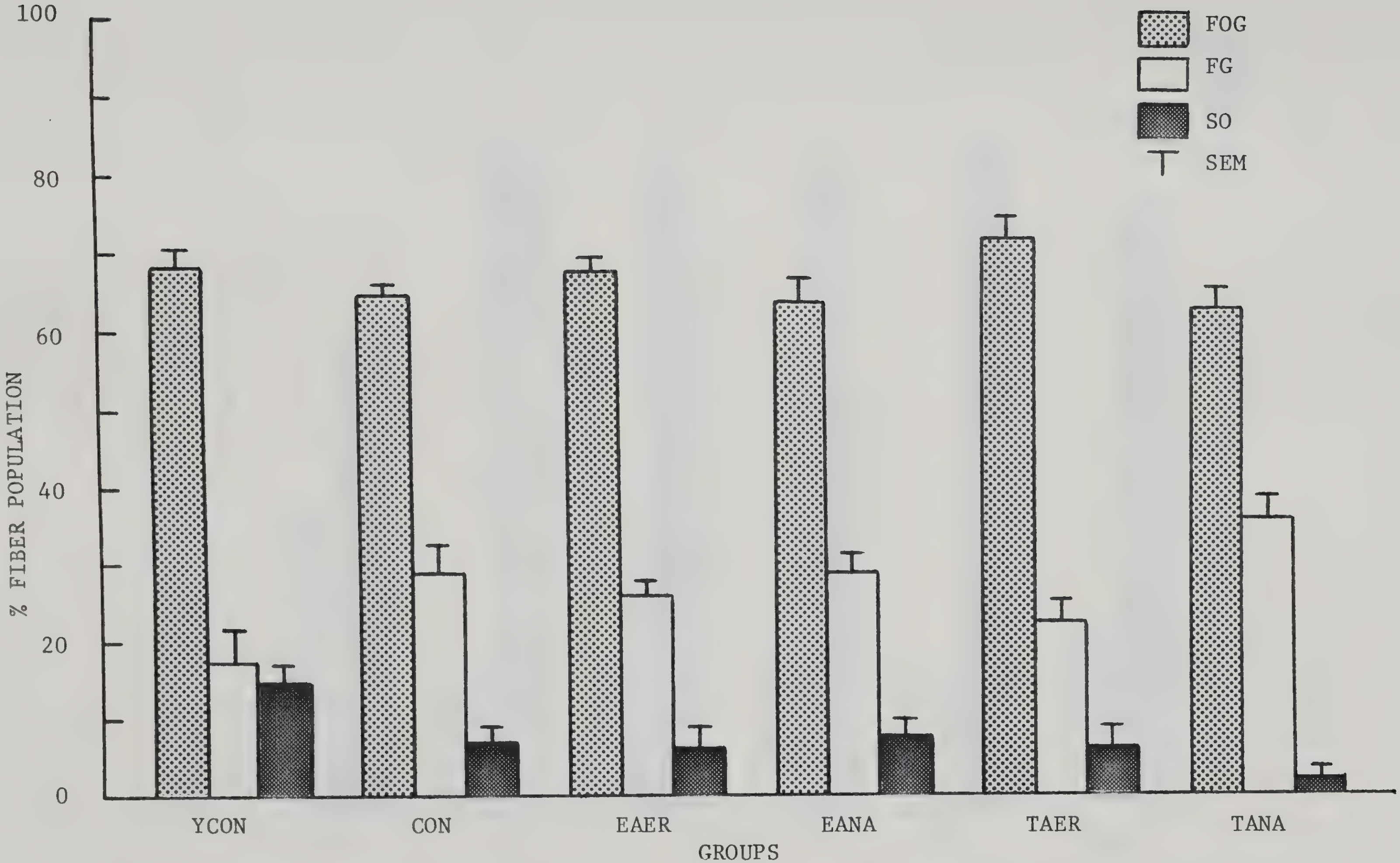

Figure 4: The effects of development and chronic physical activity (CPA) on the fiber type composition of the red vastus lateralis.

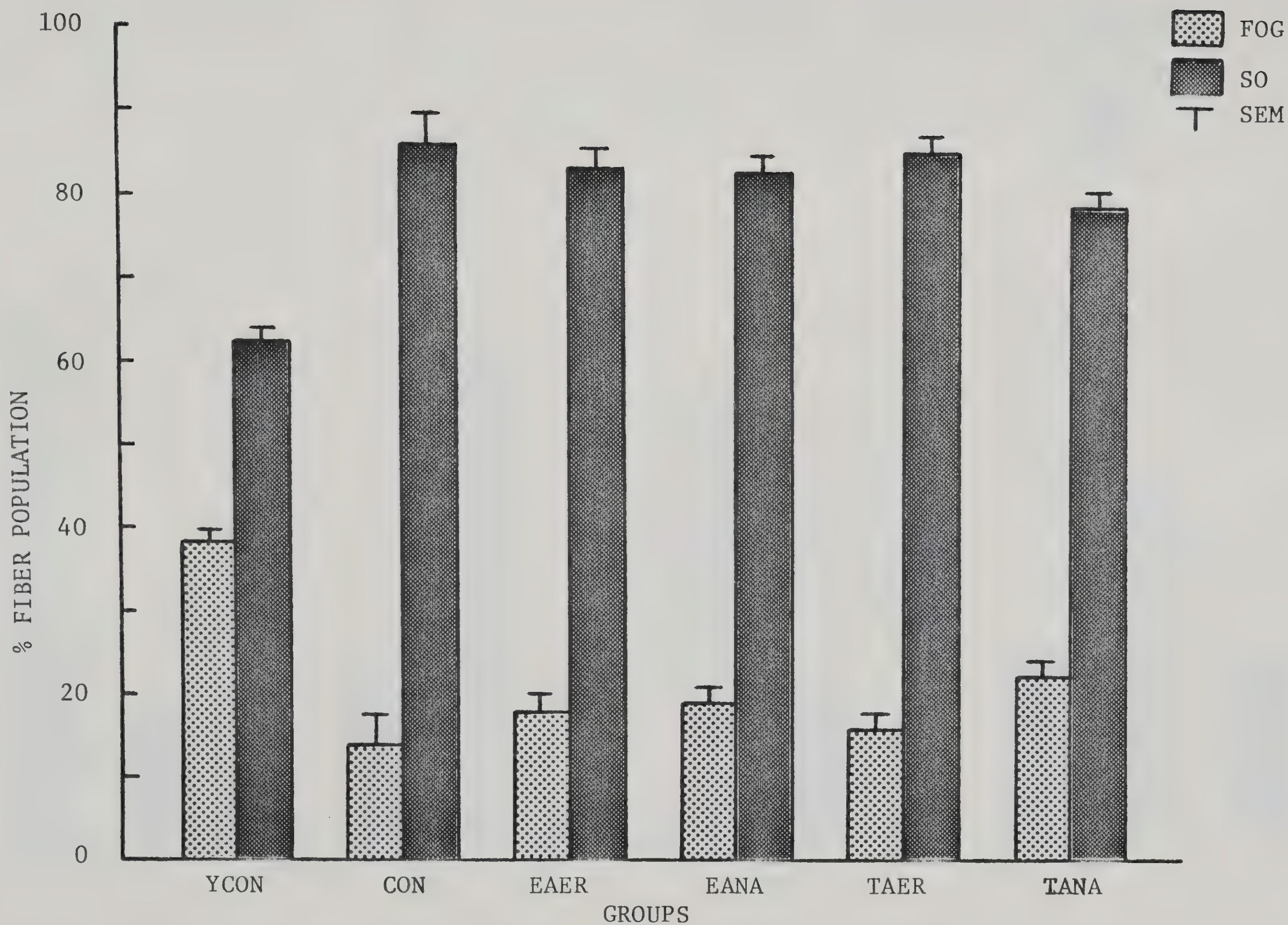

Figure 5: The effects of development and chronic physical activity (CPA) on the fiber type compositon of the soleus.

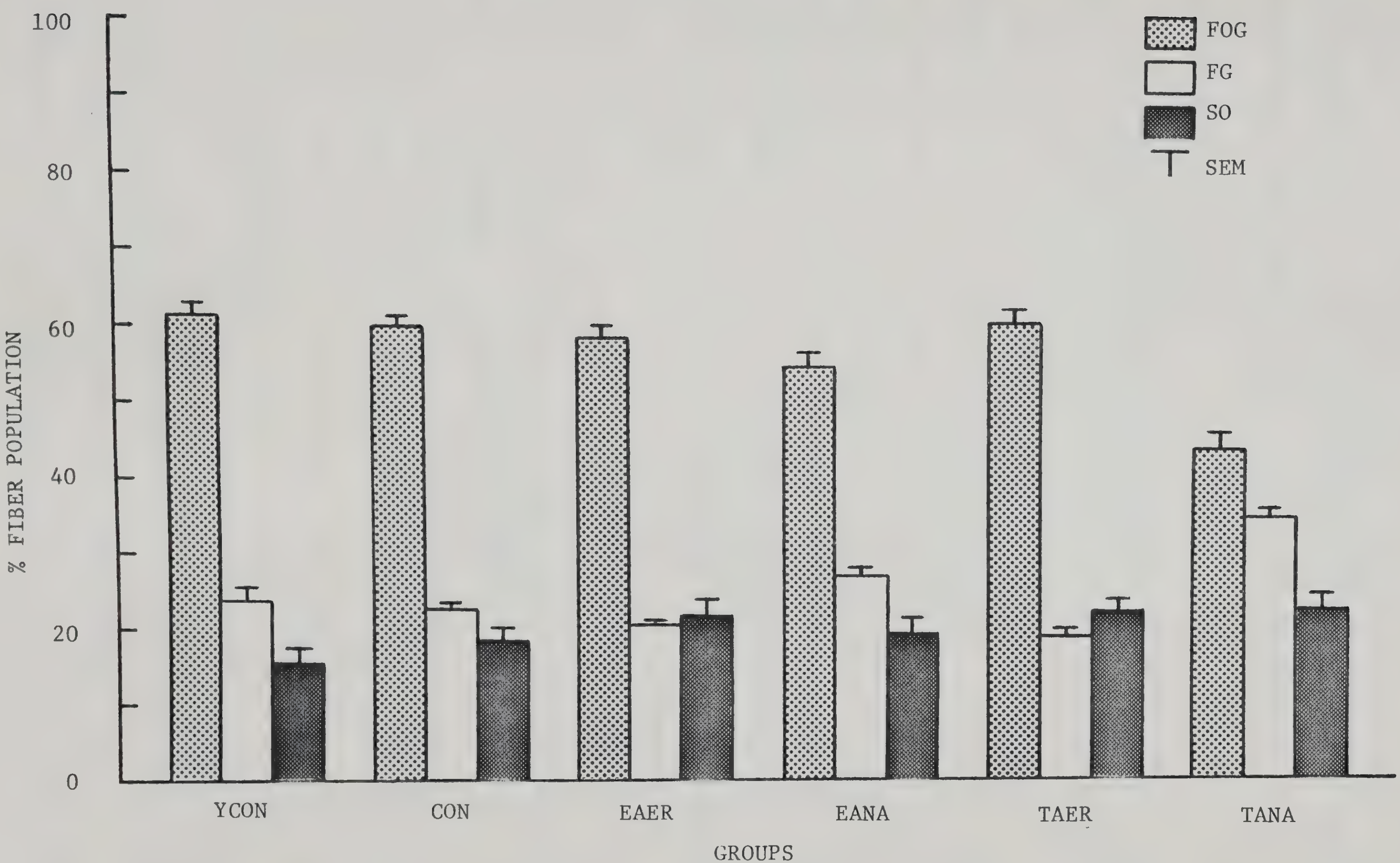

Figure 6: The effects of development and chronic physical activity (CPA) on the fiber type composition of the gastrocnemius.

population which occurred with the TANA condition of chronic physical activity. A similar developmental TANA effect was noted in the medial gastrocnemius muscle. In this case the FG fiber population increase was associated with a decrease in the FOG fiber population.

CROSS SECTIONAL FIBER AREAS

Cross sectional fiber area measurements were obtained only from sections of the gastrocnemius muscle. Mean fiber areas for each animal are recorded in Table XII, Appendix B and statistical analyses are presented in Tables XXX, XXXI and XXXII, Appendix C. The effects of development and CPA on the mean fiber areas of each group are shown in Figure 7. When the four experimental groups were compared with age-matched controls, the effects of CPA were found to be highly specific. Neither the mode nor quantity of chronic physical activity alone was found to significantly alter fiber area. However, specific combinations of these two parameters resulted in changes. The EAER group displayed significantly smaller FOG and FG fiber areas than the CON groups. All three fiber types were smaller ($p<0.05$) in the EANA group than in the CON group. In contrast, the TANA group possessed FG fibers which were significantly larger than those found in any other group. Development caused significant increases in the cross sectional area of all fiber types. The magnitude of this increase was preferentially influenced by the exposure to different types of CPA as indicated previously (comparisons with CON). In only one instance did the mode or quantity of CPA appear to selectively affect this pattern. The cross sectional area of FG fibers seemed to be preferentially increased ($p<0.05$) by training.

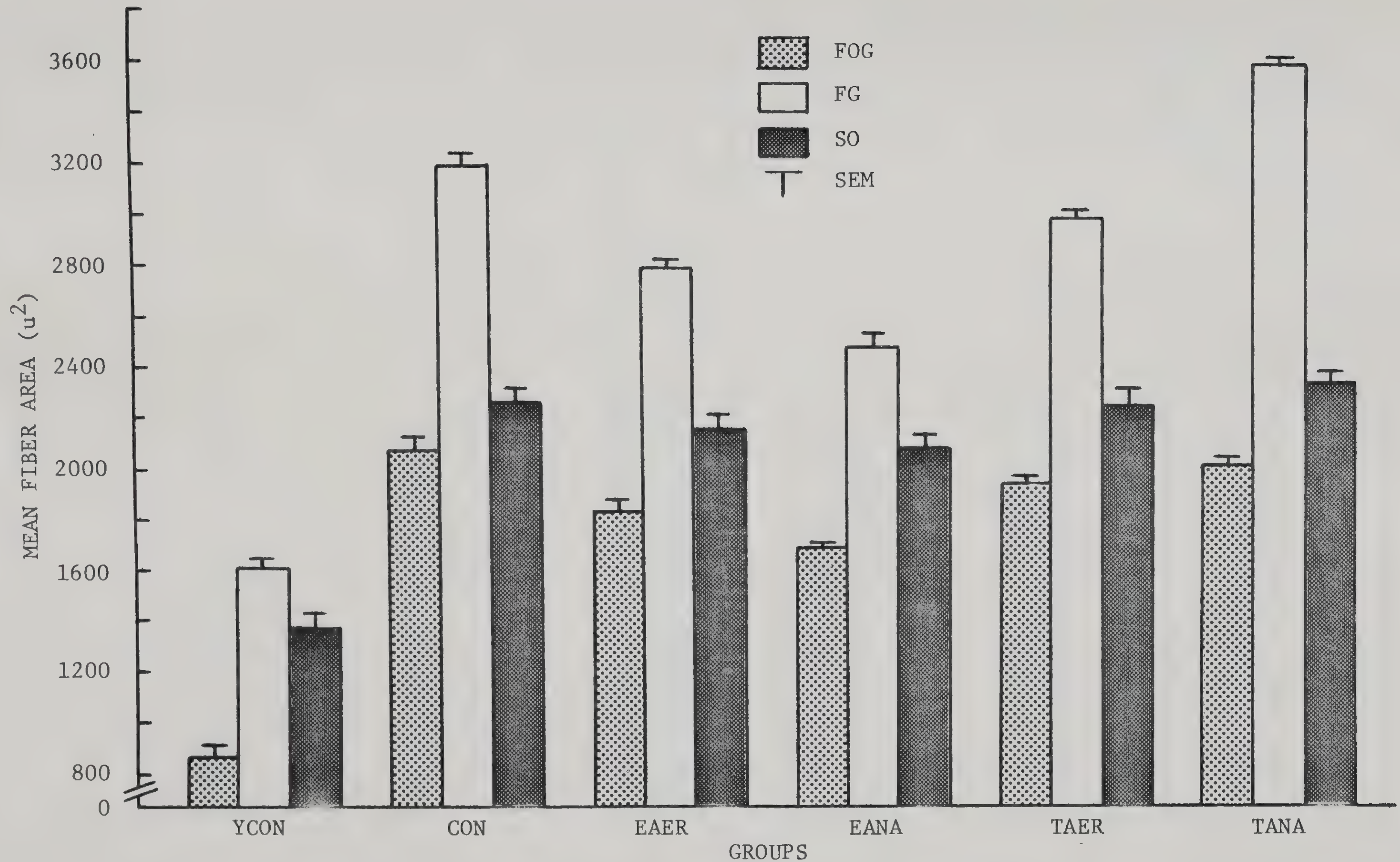

Figure 7: The effects of development and chronic physical activity (CPA) on the mean fiber areas of the gastrocnemius.

ESTIMATED FIBER TYPE CONTRIBUTIONS

Since the estimation of fiber type contribution to the total muscle is dependent upon cross sectional area, this parameter has been calculated only for the medial GAST muscle. Mean EPTM's for each animal are shown in Table XIII, Appendix B. Statistical analysis summaries are located in Tables XXXIII through XXXV, Appendix C. Figure 8 illustrates the effects of CPA and growth on the EPTM of each fiber type in all groups. The estimated proportional contribution of SO fibers to the total cross sectional area of the medial gastrocnemius muscle remained at approximately 20% in all groups. Similarly, the EPTM for FOG and FG fibers remained near 50% and 30% respectively for the YCON, CON, EAER, EANA and TAER groups. Only in the TANA group were the effects of CPA significant. In this group, the EPTM of FOG fibers decreased to 33% while a proportional increment to 47% was observed for FG fibers. Development did not elicit any alterations in the EPTM's of the three fiber types.

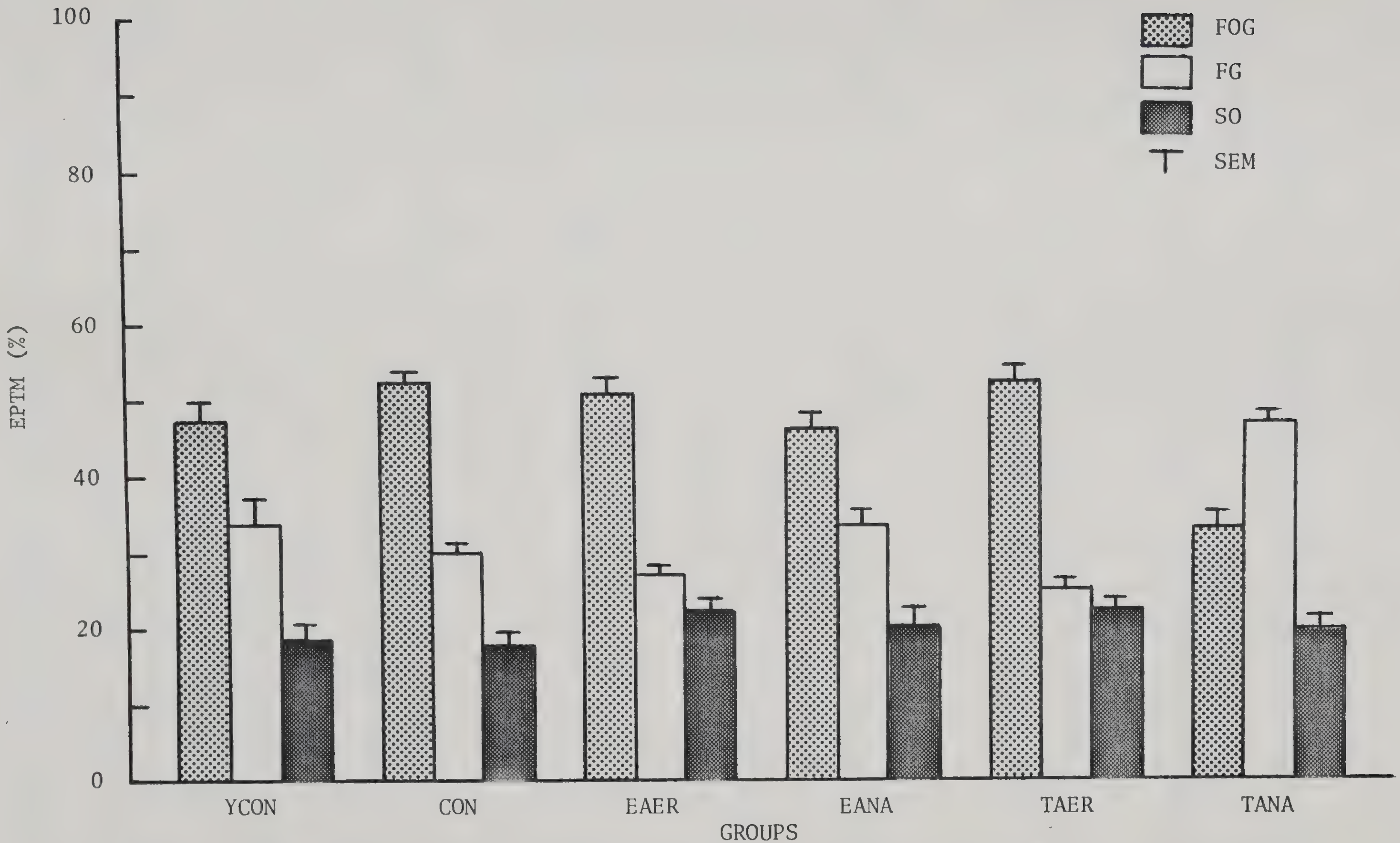

Figure 8: The effects of development and chronic physical activity (CPA) on the estimated percentage contribution to the total muscle cross sectional area (EPTM) of each fiber type within the medial gastrocnemius.

DISCUSSION

The discussion is presented under the previously used headings: Chronic Physical Activity Regimen, Body and Muscle Weights, Muscle Fiber Type Populations, Cross Sectional Fiber Areas and Estimated Fiber Type Contributions. In light of the related literature, an attempt has been made to interpret the adaptations occurring in skeletal muscle with development and chronic physical activity.

CHRONIC PHYSICAL ACTIVITY REGIMEN

The purpose of the CPA regimen was to further quantify physical activity stimuli by attempting to create groups that were both equitable and distinct. This goal appears to have been achieved. The two modes of physical activity utilized are similar in function, but unique in their motor unit recruitment patterns and metabolic requirements. A type of equality, related to the transfer of energy from a metabolic to a mechanical system, was accomplished between the two physical activity modes through the use of running distance. A distinction in stimulus quantity was realized by controlling the dosage of CPA and evidenced in the difference between total distances run. The absence of hard data, and obscurity of that which does exist, makes it nearly impossible to relate the CPA stimuli to intramuscular adaptations in a quantitative manner in previous small animal studies. Calculations reveal that the alterations seen with sprint and endurance activities by previous authors (Faulkner et al., 1971, 1972; Maxwell et al., 1973; Wilkinson et al., 1976; Mackie, 1977)

have been associated with very high quantities of activity (estimates of distances run are between 40,000 and 80,000 m).

The greater distances run by the TAER and TANA groups on the performance test indicates that the quantity of activity is associated with metabolic alterations leading to an increased work capacity. The better performance of sprint animals on the test was interesting considering that both the endurance and sprint groups covered the same total distance during the CPA regimen. It is possible that the long rest interval used in the intermittent sprint program permitted more work to be performed. Speculation may be forwarded suggesting that either the length of the recovery interval (30 sec) allowed for the removal of certain metabolites or the anaerobic CPA regimen resulted in an adaptation to acid metabolites. Also Baldwin et al. (1975) have suggested that chronic anaerobic activity may induce an increased capacity to replenish ATP and CP during recovery. It should be recognized that the quantitative comparison of fatigue onset in two different activity modes is difficult (Wenger and Reed, 1976).

BODY AND MUSCLE WEIGHTS

The increase in body weight seen with development in the present study is consistent with the literature (Bailey et al., 1973; Hubbard et al., 1974; Yager et al., 1974; Houston and Green, 1975; Gaboriault, 1977; Pitts and Bull, 1977). Endurance training was found to significantly suppress the normal developmental weight gain pattern. Similar findings have been reported by Barnard et al. (1970) and Faulkner et al. (1971) in guinea pigs and Hubbard et al. (1974), Terjung (1976),

Wilkinson et al. (1976) and Mackie (1977) in rats. In contrast, Baldwin et al. (1972, 1977) have found no decreases in body weight with chronic endurance activities. It is interesting to note that the total quantity of work performed in this study was much less than any of the other studies. Staudte et al. (1973), Houston and Green (1975), and Wilkinson et al. (1976) have shown decreased body weights with a high intensity, short duration running regimen. The non-significant decrease observed in this study parallels the findings of Baldwin et al. (1977), Jobin (1977) and Wilkinson (1977). The data of this study (CON 416.5g; EANA 373.3g; TANA 384.5g; EAER 386.2g; TAER 355.3g) suggests that body weight may be sensitive to the combined effects of mode and quantity of CPA during development. This premise is supported by Stevenson et al. (1966) who noted that the quantity of enforced running was inversely related to food intake and the finding within the present study of a difference between the weight decrements of the TAER and TANA conditions even through the quantity of work done by each group was similar. Body weight alterations accompanying CPA appear to be influenced by age, sex, and the mode, intensity, duration and quantity of the CPA stimulus.

In accordance with the literature (Faulkner et al., 1971, 1972; Maxwell et al., 1973; Houston and Green, 1975; Sillau and Banchero, 1977) a developmental increase occurred in the wet weight of the gastrocnemius muscle. No changes were noted in gastrocnemius wet weights with CPA. This is analagous to the findings of Baldwin et al. (1972, 1977), Maxwell et al. (1973), Jaweed et al. (1974), Mackie (1977) and Wilkinson (1977) on hindlimb muscle weights of chronically

active rats. Whole muscle hypertrophy of specific muscles, soleus and vastus medialis, in response to endurance programs has been reported by Maxwell et al. (1973) and Jaweed et al. (1974). Both Hubbard et al. (1974) and Mackie (1977) have noted decreased plantaris and gastrocnemius weights in response to an endurance program. The data of the present study (Table VI, Appendix B) seems to indicate that a proportional response may exist between gastrocnemius muscle weights and the quantity of chronic physical activity.

The proportional contributions of gastrocnemius muscle weight to total body weight was decreased by development, but unaltered by CPA. This developmental change is opposite to the linear relationship that Sillau and Banchero (1977) established for the relative muscle weight of the gastrocnemius during growth. In order to clarify this discrepancy, relative gastrocnemius weights were calculated from the data of Mackie (1977) and Wilkinson (1977) since no other developmental values appeared in the literature. These calculations supported the developmental increase in relative muscle weight noted by Sillau and Banchero (1977). Re-evaluation of the data of this study revealed that the discrepancy could be totally accounted for by the unusually high initial gastrocnemius weights. These weights must remain as inexplicable. The relative gastrocnemius weights reported by Houston and Green (1975) and calculated from Mackie (1977) are in agreement with the present study and indicate that no alterations in the proportional contribution of gastrocnemius muscle weight to total body weight occur with either endurance or sprint CPA.

MUSCLE FIBER TYPE POPULATIONS

The mean fiber type compositions of the twenty week control animals in the vastus lateralis white (3.5% FOG; 96.5% FG), vastus lateralis red (64.3% FOG; 29.0% FG; 6.8% SO), soleus (13.6% FOG; 86.4% SO), and medial gastrocnemius (59.3% FOG; 22.2% FG; 18.5% SO) muscles of twenty week control animals are similar to those noted by other researchers in mature rats (Edgerton and Simpson, 1969; Baldwin et al., 1972; Saubert et al., 1973; Muller, 1974; Wilkinson et al., 1976; Gaboriault, 1977; Mackie, 1977; Wilkinson, 1977). Unfortunately, very little data exists on muscle fiber composition in young animals. The observed VW (28.2% FOG, 71.8% FG) and VR (68.2% FOG; 17.4% FG; 14.7% SO) fiber compositions are analagous to those of Gaboriault (1977) while SOL (37.9% FOG; 62.1% SO) and medial GAST (60.7% FOG; 23.8% FG; 15.4% SO) composition are comparable to the data of Wilkinson et al. (1976), Mackie (1977) and Wilkinson (1977) on five week old animals.

Developmental shifts in the fiber type population of VW and SOL muscles resulted in increases of their FG and SO fiber populations respectively at the expense of FOG fibers. These alterations in fiber type with growth have been noted by several investigators (Faulkner et al., 1971; Maxwell et al.,1973; Wilkinson et al., 1976; Gaboriault, 1977; Mackie, 1977). The decline in fast twitch fiber population in the soleus during development is supported biochemically by Gutmann et al. (1974) who found that ATPase activity decreased after 30 days of age in this muscle. No developmental alterations occurred in the VR and medial GAST muscles although a slight increase (11.6%) in FG fibers with a concomitant decrement of SO fibers (7.9%) occurred

in the red vastus lateralis. The work of Faulkner et al. (1972) on 6 - to 14 - week old plantaris muscle indicated that there was a significant loss in the number of fibers per whole muscle cross section with growth. Estimates of young gastrocnemius muscle fibers per cross section have led Wilkinson (1977) to a similar conclusion. Whether these fiber losses are general or preferential in regard to fiber type is unknown. While the mechanisms controlling these developmental alterations have not been elucidated, a relationship may exist between the maturation of locomotor patterns with improved postural control and shifts in muscle fiber types.

Chronic physical activity resulted in significant alterations of the FOG and FG fiber populations in the VW and medial GAST muscles. In the VW, a significant and progressive shift in fiber population towards FOG at the expense of FG was seen irrespective of the mode of CPA. However, a more pronounced effect resulted from sprint activity. No histochemical data exists in the literature regarding the effects of CPA on the quadriceps muscles. Biochemical data (Kowalski et al., 1968; Staudte et al., 1973; Hickson et al., 1976; Baldwin et al., 1977) on the vastus lateralis white muscle indicates that increases in oxidative capacity have occurred with chronic physical activity. Staudte et al. (1973) found increases in the enzyme activities of aerobic glycolysis, but not of fatty acid oxidation after a sprint program. Baldwin et al. (1977) determined that a twofold increase in oxidative enzyme activity occurred with high intensity interval running whereas endurance activity led to a slight transient increase. These results seem to corroborate the observed fiber shift as well as the emphasized sprint mode effect. Similar fiber population

adaptations have been shown in the plantaris muscle (Edgerton et al., 1969; Faulkner et al., 1971, 1972; Maxwell et al., 1973; Wilkinson et al., 1976) which possesses a fiber type distribution analagous to the VW. An integration of the effects noted with CPA and development leads to a reassessment of the widely held 'shift in fiber type due to training' belief. Observation of the results of this study (Figure 3) have clearly demonstrated that a maintenance of the youthful fiber type distribution occurs with involvement in CPA during development in the vastus lateralis white muscle. This finding parallels those of Muller (1974), Wilkinson et al. (1976), Mackie (1977) and Wilkinson (1977). In addition, this study implies that the level of maintenance is dependent upon the quantity of CPA and influenced by the mode of CPA.

In the medial gastrocnemius only the trained anaerobic condition showed a significant FOG to FG fiber shift. Analysis revealed that the sprint mode was related to this adaptation. These results are similar to those of Gaboriault (1977), Jobin (1977), Mackie (1977) and Wilkinson (1977) but contrary to those of Saubert et al. (1973). The divergent results of Saubert et al. (1973) and Fitts et al. (1973), who found no alteration, may be due to their use of adult animals. While endurance activity has been shown to increase FOG and decrease FG fiber populations in gastrocnemius muscle (Barnard et al., 1970; Muller, 1974), both this study and Mackie (1977) have observed no change. In the medial GAST, sprint activity seems to accentuate rather than maintain the developmental pattern in proportion to the quantity of CPA.

In both the vastus lateralis red and soleus muscles no

statistically significant alterations in fiber type distributions occurred in response to CPA. However, patterned responses to the CPA stimuli were evident. In the VR increased quantities of aerobic CPA increased the FOG population at the expense of FG (64.3%, 67.6%, 71.6% for FOG in CON, EAER and TAER respectively) while the sprint mode showed an opposite effect (29.0%, 29.0%, 35.4% for FG in CON, EANA and TANA respectively). In soleus, increased quantities of the sprint mode tended to maintain the youthful fiber pattern (37.9%, 21.8%, 18.5%, 13.6% for FOG in YCON, TANA, EANA and CON respectively). Biochemical evidence on the VR (Baldwin et al., 1972; Saubert et al., 1973, Terjung, 1976; Baldwin et al., 1977) indicated that oxidative and glycolytic capacities were enhanced by endurance and sprint programs respectively. The expectation of an intramuscular localization was not borne out and this is in accord with the one report in the literature (Saubert et al., 1973). Most researchers have not seen significant changes in soleus muscle composition with either endurance (Edgerton et al., 1969; Edgerton et al., 1972; Maxwell et al., 1973; Mackie 1977, or sprint (Saubert et al., 1973) activities. However, both aerobic (Wilkinson et al., 1976) and anaerobic (Wilkinson et al.,1976; Mackie, 1977) programs undertaken during growth have been shown to reduce the developmental decrement in FOG fiber population. Support for this premise is provided by Baldwin et al. (1975b) who found increased actomyosin ATPase levels in the soleus muscles of rats run aerobically throughout youth.

In no instance were the SO fiber population of the four muscles affected by CPA. This indicates that the contractile properties of motor units may not be converted by physical activity. It must be remembered when interpreting the data that a gradient of metabolic

potential exists. Alteration of mitochondrial and enzyme concentrations and enzyme activities within a muscle fiber will determine its oxidative and glycolytic potential and consequently its classification. Therefore, FOG to FG shifts and vice versa only infer a change in metabolic properties -- not a creation or loss of fibers.

CROSS SECTIONAL FIBER AREAS

As stated previously, alterations within the structural protein components of skeletal muscle may occur as an adaptive response to chronic physical activity. In an attempt to ascertain if preferential adaptations of this type resulted from the CPA regimen, the cross sectional areas of FOG, FG and SO fibers were measured in the medial gastrocnemius muscle. The increases in fiber area (139%, 98% and 65% for FOG, FG and SO fibers respectively) evidenced between seven and twenty weeks of age are indicative of a general developmental hypertrophy. This observation corresponds with those of Faulkner et al. (1972), Maxwell et al. (1973), Burleigh (1974), Sillau and Banchero (1977) and Wilkinson (1977). A linear relationship has been shown between body weights, muscle weights and fiber areas during development (Muller, 1975a, 1975b; Sillau and Banchero, 1977) with the slope dependent upon the growth rate of the specific muscle.

All three fiber types within the EANA group and the FOG and FG fibers in the EAER were significantly smaller than those of age matched controls. This seems to indicate that low quantities of CPA may moderate the general hypertrophic response associated with development. The data of Faulkner et al. (1971, 1972) could be considered supportive, however, they administered a much greater quantity of CPA and used

guinea pigs. An interesting interpretation arises from the work of Walker (1966). He suggested that chronic physical activities of short duration resulted in a reduction of the hypertrophic response which was maintained over time. The short CPA duration and low frequency attendant to the EAER and EANA conditions may have exerted such an influence. Another possible mechanism must be considered when interpreting these observations. It is possible that a hypertrophic effect related to the quantity of CPA occurred as indicated by the greater cross sectional areas of all fiber types under trained versus exercised conditions within both the aerobic and anaerobic modes. This effect may be masked by the composition of the age-matched control muscle fibers. In essence, it has been assumed that the cellular constituents of muscle fibers are proportionally similar and that any observed changes in cross sectional area must be due to alterations within the structural protein component. However, it may be speculated that the large cross sectional areas present in the age-matched sedentary control group arose from a greater storage of intramuscular lipids and would not be attributable to an alteration within the structural protein component.

The significant increment of FG fiber size in the TANA group is supportive of the sprint-elicited hypertrophy noted by Wilkinson (1977). Since the cross sectional area is directly related to the force exerted by a muscle fiber (Close, 1972), this adaptation appears to have occurred to enable the gastrocnemius muscle to perform repeated forceful contractions. Training appeared to be significantly related to increased FG fiber area, however, close examination (Figure 7) revealed

that the large increase in the TANA group was responsible for this observation. The endurance mode of CPA appears to have no influence upon fiber hypertrophy in developing gastrocnemius muscle. This is compatible with the results obtained by Maxwell et al. (1973), but divergent from those of Carrow et al. (1967) and Edgerton et al. (1972) on various muscles. The pattern of adaptations shown in response to the various CPA stimuli in the present study seems to fit in well with the existent literature.

ESTIMATED FIBER TYPE CONTRIBUTIONS

The EPTM combines the knowledge of fiber distribution and area to create a variable which more accurately portrays the functional contribution of each fiber type to the muscle as a whole. Table XXXVIII, Appendix E summarizes the pertinent data and relationships associated with EPTM in the present study and allows comparison with the data of Wilkinson (1977) and Sullivan and Armstrong (1978).

No change in the EPTM's of the three fiber types was observed with development in the present study. The EPTM's of the mature sedentary rat (CON) are similar to those reported by Wilkinson (1977) and Sullivan and Armstrong (1978). The differences noted in the data of Sullivan and Armstrong (1978) are primarily due to the use of Sprague-Dawley rats which are of a more aerobic nature than the Wistar strain. Similarly, no alterations were noted in the EPTM of SO fibers under any of the CPA conditions. The EPTM's for FOG and FG fibers within the CON, EAER, EANA and TAER groups remained near 50% and 30% respectively. In the TANA group a dramatic shift was apparent. Here the EPTM of FOG fibers decreased to 33% while the FG fibers showed a proportional increase to 47%. This shift is similar to that disclosed

by Wilkinson (1977). The magnitude of this shift is supported by the indication of significant sprint and training effects which are due solely to the TANA group. This corroborates both the FG muscle fiber distribution and hypertrophy results and supports the contention of selective metabolic and structural adaptations within specific muscle fiber types in response to a functional overload of those motor units during CPA.

SUMMARY

1. Large developmental changes occurred in body weight, muscle weight, relative muscle weight, fiber type composition, and fiber area, but not in the estimated proportional fiber type contribution to total muscle cross sectional area with normal growth of sedentary rats.

2. Selective combinations of mode and quantity preferentially affected body weight, fiber type composition, fiber area, and the estimated proportional fiber type contribution to total cross sectional area, but not muscle weight or relative muscle weight after chronic physical activity in young animals. The occurrence, direction, and magnitude of these alterations was highly specific in different muscles and maintained or accentuated normal developmental patterns.

3. A general pattern indicating that greater alterations occurred with sprint as compared to endurance and with an increased quantity of chronic physical activity was evidenced at the cellular level.

4. The results imply a specificity in adaptation which appears to be dependent upon the intensity, duration, frequency and quantity of a chronic physical activity and consequently of the motor unit recruitment.

5. In order to understand the mechanisms underlying adaptation in skeletal muscle and realize applicability, further quantification of chronic physical activities is required.

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APPENDIX A

REVIEW OF LITERATURE

CLASSIFICATION OF FIBER TYPES

The oldest and simplest classification of skeletal muscle was based upon its gross appearance. Two distinctly different types of fibers were observed and labelled as either red (dark) or white (light). With the advancement of histochemical and biochemical techniques, many physiological studies determined that this classification was not adequate as there appeared to be more than two fiber types which correlated with various neural and metabolic parameters. This led to a plethora of proposed classification schemes (Engel, 1962; Stein and Padykula, 1962; Romanul, 1964; Henneman and Olson, 1965; Padykula and Gauthier,1967; Brooke and Kaiser, 1970; Yellin and Guth, 1970; Barnard et al., 1971; Peter et al., 1972). Peter et al. (1972) classified muscle fibers as either fast twitch - oxidative - glycoltyic (FOG), fast twitch - glycolytic (FG), or slow twitch - oxidative (SO) according to their inherent neural and metabolic profile. The functional relevance of this nomenclature has led to its widespread use in clarifying the effects of physical stimuli upon skeletal muscle as well as fiber type identification in many mammalian species including rats (Edgerton et al., 1969; Ariano et al., 1973; Wilkinson et al., 1977), guinea pigs (Barnard et al., 1970; Peter et al., 1972; Maxwell et al., 1973), cats (Ariano et al. 1973; Burke et al., 1973; Gonyea and Ericson, 1976), lions (Armstrong et al., 1977), rabbits (Peter et al., 1972), horses (Lindholm et al., 1975), lesser bushbabies (Edgerton et al., 1972; Ariano et al., 1973)

and humans (Edgerton et al., 1975; Prince et al., 1976, 1977). Information on the biochemical, histochemical and morphological properties of the three fiber types and the relationships between classification systems has been summarized by Close (1972) and Peter et al.(1972).

NORMAL SKELETAL MUSCLE DEVELOPMENT

Much of the information in this section is a synthesis of the work of Close (1972) and Burleigh (1974). Muscle fibers are formed in the foetus by the fusion of mononucleate myoblast cells into two types of myotubes, primary and secondary. It has been shown in mixed muscle that primary myotubes develop first and then the secondary myotubes grow around them. Neonatally, both types of myotubes demonstrate slow myofibrillar ATPase activity however, a differentiation occurs with ontogeny. Postnatally, in the rat, some primary myotubes display a maintenance (Brown, 1973) or decrease (Gutmann et al., 1973) in their myofibrillar ATPase activity until three to five weeks of age when a stabilization of twitch time occurs. Other primary myotubes and all secondary myotubes display increases in myofibrillar ATPase activity which continue through to maturity. This neural divergence is paralleled by and possibly controls metabolic changes. Histochemically, primary myotubes demonstrate the acquisition of oxidative properties while secondary myotubes develop glycoltyic characteristics after a transitional oxidative phase. It can be seen that the neural and metabolic differentiation of primary and secondary myotubes leads to the development of SO and FOG, and FG muscle fibers respectively.

Growth related shifts in fiber composition have been observed

during development. Faulkner et al. (1971) and Maxwell et al. (1973) have noted an increase in the population of FG fibers at the expense of FOG fibers in guinea pigs between 6 and 14 weeks of age. Wilkinson et al. (1976) noted a similar alteration in the plantaris III of rats but not plantaris II. Mackie (1977) also found no change in the plantaris II composition of rats between 5 and 15 weeks of age. A reduction of the FOG fiber population with a corresponding increment in SO fibers has been shown in developing guinea pig and rat soleus muscles (Maxwell et al., 1973; Wilkinson et al., 1976; Gaboriault, 1977; Mackie, 1977; Sillau and Banchero, 1977). A developmental shift from FG fibers towards FOG fibers in rat tibialis anterior muscle was observed by Sillau and Banchero (1977) while Maxwell et al. (1973) saw no alterations in the predominantely fast twitch psoas muscle of guinea pigs. Gaboriault (1977) recorded increases in the FG fiber populations of rat vastus lateralis red and vastus lateralis white muscles at the expense of FOG fibers after 13 weeks of growth. Both Wilkinson (1977) and Sillau and Banchero (1977) found a decrease in the FG fiber population with a concomitant increase in the SO fiber type within the medial gastrocnemius muscle of developing rats. Mackie (1977), however, observed an increase in the FG fiber population of this muscle with a decrease in the FOG fiber population and no alteration of the SO fiber type.

Myotubular development and differentiation have also been correlated with certain morphological characteristics. In the embryo, secondary myotubes are smaller than primary myotubes. With subsequent development and neural differentiation, a greater hypertrophy is noticed in secondary myotubes which may be attributed to the development of

more forceful contractions in these fibers. The failure of primary myotubes to demonstrate large increments in size may be attributed to their high mitochondrial concentrations. The oxidation of carbohydrates and amino acids for energetic purposes may lead to a decrease in their availability to ribosomes for protein synthesis thereby reducing the potential for hypertrophy. This pattern continues postnatally and results in FG fibers being much larger in size than either FOG or SO fibers (Close, 1972; Maxwell et al., 1973). As the animal grows, skeletal muscles adapt by increasing the cross sectional area of the whole muscle. This arises via two mechanisms. Hyperplasia occurs through the differentiation of myoblasts into myofibrils until just after birth (Chiahulas and Pauly, 1965; Curless and Nelson, 1976) when a slow loss in the number of fibers within a muscle develops until maturity (Maxwell et al., 1973). Secondly, a rapid hypertrophy of all three fiber types starts after birth and assymptotes following maturity (Faulkner et al., 1972; Maxwell et al., 1973; Muller, 1975; Curless and Nelson, 1976). While the growth rate varies depending upon the muscle involved, linear relationships have been found between body weights, muscle weights and cross sectional fiber areas (Faulkner et al., 1971; Bailey et al., 1973; Hubbard et al., 1974; Sillau and Banchero, 1977).

The neural, metabolic and morphological characteristics of a muscle are intrinsically related to the muscles' function. Henneman and Olson (1965) have shown this relationship in plantarflexors of the cat foot - the medial gastrocnemius and soleus. The more peripheral medial gastrocnemius is composed predominantly of fast contracting fibers of a glycolytic nature which run obliquely to the long axis of

the leg and develop high tensions over a short range of motion for short periods of time. In contrast, the soleus possesses slow contracting, highly oxidative fibers which run parallel to the long axis and generate low tensions over a large range of motion for long periods of time. This evolutionary adaptation of complementary muscles enables the animal to perform locomotive and postural functions with a minimum of energy expenditure and maximal efficiency. The extent of their functional adaptations is borne out further when the capabilities and localization of specific fiber types is considered. Fast twitch- glycolytic fibers develop high mechanical tensions and are often found in the peripheral limb muscles associated with locomotion (Henneman and Olson, 1965; Close, 1972; Ariano et al., 1973; Burleigh, 1974). Fast - oxidative - glycolytic fibers have lower tension producing capabilities and are associated with frequent, highly repetitive movements such as those of small animal diaphragms (Henneman and Olson, 1965; Burleigh, 1974). Slow twitch - oxidative fibers also create low mechanical tensions and are commonly found in posture related muscles (Henneman and Olson, 1965; Close, 1972; Ariano et al., 1973; Burleigh, 1974). Affirmation of these functional relationships is provided by the observations of Ariano et al. (1973) which show a high similarity in the fiber type distributions of the same muscle between different species. The progressive neural, metabolic and morphological changes seen in skeletal muscle fiber types during development may reflect the effects of neural maturation and increased body weight upon the accruement of mature locomotor and postural patterns. The rate and magnitude of these alterations vary among mammalian species depending upon the genetic

potential, gestation period, age of maturation and ultimate body weight of the animal (Chaikulas and Pauly, 1965; Henneman and Olson, 1965; Close, 1972, Maxwell et al., 1973; Burleigh, 1974; Sillau and Blanchero, 1977).

METABOLIC ADAPTATIONS TO CPA IN SKELETAL MUSCLES

Effects of Endurance Activities

Numerous researchers have investigated the effects of chronic endurance activities upon the energy production capabilities of skeletal muscle through the biochemical assessment of specific metabolic protein components in muscle homogenates. Kowalski et al. (1969) observed increases in the activities of phosphorylase, succinate dehydrogenase and cytochrome oxidase in the whole quadriceps muscle of rats exposed to an endurance program between 14 and 20 weeks of age. Increases in oxidative enzymes (fumarase, succinate dehydrogenase, cytochrome oxidase and citrate synthase) were reported by Benzi et al. (1975), Hickson et al. (1976) and Terjung (1976) in many different muscles (soleus, plantaris, gastrocnemius, vastus lateralis red and vastus lateralis white) of rats involved in endurance activities through their developmental period. Baldwin et al.(1972) reported increases in the capacity to oxidize pyruvate and palmitate; cytochrome c concentration; and activity levels of cytochrome oxidase, carnitine palmityltransferase and citrate synthase in the soleus, mixed quadricep and vastus lateralis red and white muscles of young male rats after a twelve week endurance program. Baldwin et al. (1977) showed that no sex difference existed by running young female rats for ten weeks. They found increasing

levels of citrate synthase and hexokinase in soleus and red vastus muscles throughout the endurance program. In the vastus lateralis white, both enzymes showed a large initial increase followed by a slow, steady decrease after the second week. An eight week endurance program using young rats was found to increase cytochrome c concentrations in the soleus and gastrocnemius but not plantaris muscle (Hubbard et al., 1974). A four week continuation of this program after maturity led to an increase only in the soleus muscle. Adult guinea pigs were run aerobically for either 9 or 18 weeks by Barnard et al. (1970). Increased mitochondrial protein concentrations per gram of muscle were noted only after 18 weeks of activity. Edgerton et al. (1972) administered a six month endurance program to adult lesser bushbabies (Galago senegalensis - a primate). No differences were noted in glycolytic enzyme levels (phosphorylase and lactate dehydrogenase) within the vastus lateralis and semimembranosus muscles but oxidative enzyme levels (cytochromes a and c) increased. In general, the literature demonstrates increases in oxidative enzyme capabilities with chronic endurance activities. Certain response specificities have been noted with respect to age, glycolytic enzymes and the muscle studied. Cross-sectional studies of endurance athletes (Gollnick et al., 1972; Costill et al., 1976) and the controlled administration of endurance activity (Gollnick et al., 1973; Andersen and Henriksson, 1977) have shown that adult human skeletal muscle responds to chronic aerobic activity in a similar manner.

Histochemical procedures have been utilized to isolate the location of metabolic responses to chronic physical activities within skeletal muscle. Edgerton et al. (1969) and Maxwell et al (1973)

have demonstrated increases in the FOG fiber population at the expense of FG fibers in the plantaris muscles of young rats on endurance swimming or running programs. However, no shifts in fiber population were seen in soleus and psoas muscles. No fiber population alterations occurred in the plantaris or soleus muscles of adult lesser bushbabies exposed to a six month aerobic running program (Edgerton et al., 1972). A FG to FOG fiber type shift did occur in the tibialis anterior muscle. Similar increases of FOG fiber populations and decreases in the number of FG fibers were shown in the plantaris and diaphragm muscles of young endurance run guinea pigs by Faulkner et al. (1971, 1972). They also determined that 16 weeks of post maturity detraining resulted in a reversion of the plantaris fiber population to control values. Barnard et al (1970) found the same pattern of FOG, FG fiber type alteration in both the white and red portions of adult guinea pig medial gastrocnemius muscles after an 18 week endurance running program. An aerobic running program did not alter the fiber type distribution in the gracilis and biceps femoris muscles of miniature pigs (Fitts et al., 1973). The above researchers have based their observations and subsequent interpretations upon the comparison of active animals against age-matched sedentary controls. This procedure, as indicated by Wilkinson et al. (1976), may lead to erroneous conclusions regarding the effects of chronic physical activity upon muscle fiber populations. In comparison to age-matched controls, Wilkinson et al. (1976) reported a FG to FOG fiber shift in the plantaris and a SO to FOG fiber shift in the soleus muscles of 15 week old rats subjected to a 10 week aerobic running program. When the fiber compositions of the active rats

were compared with those of 5 and 10 week controls it became evident that endurance activity had decreased the magnitude of normal developmental alterations. While the work of Mackie (1977) showed no changes in soleus, plantaris II and medial gastrocnemius muscle fiber mosaics with chronic endurance running, when contrasted to age-matched controls, comparison with young control animals revealed a tendency for the youthful fiber type pattern to be maintained. This data lends credence to the hypothesis that chronic physical activity during development leads to a preservation of juvenile fiber type patterns rather than an outright shift in fiber type distributions.

Histochemical data on humans reveals that different patterns of metabolic adaptation may exist at the muscle fiber level in this species even though adaptations at the biochemical level are analagous to those of other species. Gollnick et al (1972) found that athletes engaged in endurance events showed mean SO fiber populations of approximately 60% in the deltoid and vastus lateralis muscles while untrained subjects displayed an average SO fiber type of 46% and 36% respectively in those two muscles. Higher SO fiber populations were also observed by Costill et al., (1976) in both male distance runners (69.4%) and female middle-distance runners (60.6%) than in untrained males (52.6%) and females (51.0%). Gollnick et al (1972) noted an insignificant increase in SO fiber population (32% to 36%) after a five month aerobic bicycle ergometer program in middle-aged men. All three of these studies performed histochemical procedures which led to muscle fibers only being classified as either slow twitch or fast twitch. The biochemical analyses done in these studies indicated nearly parallel

increases in the oxidative capabilities of the two fiber types. Thus, alterations in the intramuscular localization of the observed metabolic adaptations may have been masked by the histochemical methods. In more recent work, Prince et al. (1976, 1977) have demonstrated that both male and female endurance athletes exhibit different fiber type patterns than untrained subjects of the same sex in the vastus lateralis muscle. In contrast to previous investigators, Prince et al. (1976) found that male endurance athletes have similar levels of SO fibers (10% greater) than control subjects but exhibit a marked reduction (21.7%) in FG fiber population. The existance of a fiber population exhibiting fast twitch characteristics and a moderate oxidative capacity (called "transitional") only in the running group suggested that an incomplete shift from FG fibers towards FOG fibers had occurred. This pattern of metabolic adaptation is also apparent in female endurance athletes (Prince et al., 1977) where a more complete shift of FG fibers towards FOG fibers was noticed. The large number of factors related to the measurement of metabolic adaptations in humans precludes easy quantification of their intramuscular localization.

Effects of Sprint Activities

There is a scarcity of research concerning the effects of chronic sprint activities on skeletal muscle fiber types. After a three week high-intensity running program, Staudte et al. (1973) found that soleus and rectus femoris muscles of young rats displayed higher glycolytic and glycogenolytic enzyme activities. Hickson et al. (1976) found increased glycolytic enzyme activities in plantaris, soleus and white

vastus lateralis muscles. These enzyme adaptations were similar in both endurance and sprint trained animals after 8 and 16 weeks of running. In comparing nine weeks of high speed interval and steady state running, Baldwin et al. (1977) noted similar increases in citrate synthase and hexokinase activity in soleus and red vastus lateralis muscles. In the white vastus lateralis, a transient increase resulted from the steady state situation while the sprint activity caused a twofold increase in enzyme activity. Saubert et al. (1973) found a FG to FOG shift in the white portion of the gastrocnemius from rats subjected to an eleven week sprint program. No alterations were seen in the fiber composition of soleus, red vastus lateralis or red gastrocnemius muscles. Glycolytic enzyme capacity was elevated only in the soleus muscle. From these results, they suggested that most skeletal muscles have an anaerobic capacity which allows short-term, heavy intermittent work demands to be met without adaptation. Fitts et al. (1973) found no changes in minature pig biceps femoris or gracilis muscles in response to a chronic sprint protocol. Wilkinson et al. (1976) saw no change in the young rat soleus muscle fiber pattern following a 10 week sprint program. However, a significant shift from FOG to FG fibers occurred in the plantaris III muscle region. After sprint running rats from age five-to fifteen-weeks, Mackie (1977) found no alterations in the plantaris muscle but a FOG to FG shift in the gastrocnemius. The normal aging pattern of the soleus was altered and resulted in a maintenance of the FOG fiber population. Wilkinson (1977) corroborated the shift toward FG fibers in the young rat gastrocnemius in a study which provided high speed interval running for 20 weeks. Jobin (1977)

noted a shift towards high glucose phosphorylation in the gastrocnemius muscles of young rats sprint run for six weeks. The enzymatic adaptations were accompanied by a shift from FOG to FG fiber types. It is difficult to generalize from a small data base, however, sprint activities appear to enhance glycolytic enzyme capabilities thereby creating shifts towards a more glycolytic fiber distribution.

Comparable human data is virtually non-existent. The effects of treadmill sprint training for 8 weeks were measured by Thorstensson et al. (1975) in the vastus lateralis muscle of males. The capacity to resynthesize ATP from ADP and CP was enhanced, but the muscle fiber type distribution remained the same. Unfortunately, muscle fibers were only classified as slow or fast twitch thereby negating the measurement of any metabolic shift within the fast twitch fiber population. In a cross-sectional study, Costill et al. (1976) found that sprint runners of both sexes had a much higher proportion of their gastrocnemius muscle composed of fast twitch fibers. Again, only a slow twitch, fast twitch classification was used.

STRUCTURAL ADAPTATIONS TO CPA IN SKELETAL MUSCLES

The hypertrophic response of skeletal muscle to CPA stimuli is well established (Gordon 1967; Goldberg et al., 1975). Tremendous increases in whole muscle and individual fiber size have been demonstrated through unilateral compensatory overloads (Tomanek, 1974; Goldberg et al., 1975; Baldwin et al., 1976). Inducement of this type of overload is achieved through the denervation, tenotomization or extirpation of synergistic muscles. While these procedures demonstrate the great adaptability of

skeletal muscle it is questionable whether the changes noted are paralleled in naturally functioning muscle groups.

Isometric and isotonic weight lifting programs have been shown to produce increases in strength, whole muscle size and fiber size in rats and cats (Gordon, 1967; Gonyea and Bonde-Petersen, 1978). The constant or decreased muscle weights and whole muscle areas sometimes seen with increased strength in these types of programs has been associated with selective muscle fiber hypertrophy, usually of the FG fiber (Gordon et al., 1967b; Muller et al., 1975b). Data collected from human studies (Thorstensson et al., 1975; Costill et al., 1976, Prince et al.,1976) demonstrates responses analogous to those shown in small animal models. Recent advances in the normalization (Muller, 1975a) and quantification (Gonyea and Ericson, 1976) of data evolved from such hypertrophic studies suggests and supports the existence of a temporal sequencing of metabolic and morphological adaptations to these modes of CPA (Muller, 1974, 1975a, 1975b; Gonyea and Ericson, 1976). This theory suggests that physiological and biochemical parameters are altered initially with morphological changes occurring later. However, changes in fiber type area will be evidenced prior to alterations in fiber distributions (Muller, 1974, 1975b).

Since sprinting involves forceful muscular contractions analogous to those of isometric weight lifting, similar structural adaptations may occur in response to chronic sprint activities. Hickson et al. (1976) showed no difference between the fiber areas of rats sprint trained for 8 weeks and age matched controls. While fibers were selected from various regions of the plantaris, soleus and gastrocnemius muscles, no

fiber typing was done. This procedure would mask the effects of selective hypertrophy. Wilkinson (1977) demonstrated selected SO and FG hypertrophy in response to sprint activity. Decreased SO fiber populations over time were offset by concomitant hypertrophy in the remaining SO fibers. The FG fiber hypertrophy was noted only after an initial increment in its percentage distribution. After an eight week treadmill sprint program, Thorstensson et al. (1975) found increased areas in both fast twitch and slow twitch vastus lateralis muscle fibers. Unfortunately, no metabolic characterization was done in their fiber typing procedures. No generalization on the relationship between structural adaptations and the sprint CPA mode can be forwarded due to the paucity of research.

Endurance activities are usually associated with metabolic rather than morphological adaptations. Carrow et al. (1967), Gordon et al. (1967a) and Faulkner et al. (1971, 1972) used only a red or white fiber classification system and demonstrated divergent responses to endurance running programs. Carrow et al. (1967) found increased size in both red and white fibers under voluntary and forced running conditions in young rat gastrocnemius muscle. In contrast Faulkner et al. (1971, 1972) observed in young guinea pig plantaris muscle a decreased area in both fiber types after eight weeks of running in comparison to age matched controls. Gordon et al. (1967a) found a dissimilar response pattern consisting of decreased red fiber size but increased white fiber size in mature rats after chronic endurance swimming. A muscle specific response was found after a six month treadmill program by Edgerton et al. (1972) in adult Galagos senegalensis. No alterations

in fiber size were apparent in the tibialis anterior muscle. A selective FOG hypertrophy was noted in the soleus muscle. In the plantaris, FOG and SO fiber diameters were increased while the FG fiber size remained constant. Maxwell et al.(1973) located an increase in soleus SO fiber area in young rats exposed to an eight week running regimen. However, no variation existed in the three fiber types of plantaris muscle when compared to control animals. Using mice, Walker (1966) determined that the duration of endurance activity was more influential than intensity in producing muscle fiber hypertrophy. Again geralizations are difficult due to the small amount of research. Indications point to the possibility of selective hypertrophy of FOG and/ or SO fibers in specific muscles with endurance CPA of a long duration.

In humans, the responses appear to be just as specific. Gollnick et al. (1973) showed an increase in slow twitch fiber area, but not fast twitch in the vastus lateralis muscle after a five month bicycle ergometer program. Costill et al. (1976) noted that long distance runners possessed much larger slow and fast twitch fibers in the gastrocnemius muscle than untrained subjects. Punch biopsies from the vastus lateralis muscle of male distance runners contained FOG and SO fibers which were slightly larger than those from controls (Prince et al., 1976). In a further study, Prince et al. (1977) found that female field hockey players had larger SO, FOG and FG fibers than sedentary subjects.

When considering structural adaptations to CPA, the possible involvement of two other general mechanisms exists. It is possible for alterations to occur in the subcellular localization of protein in

conjunction with an increment in strength, but show no evidence of hypertrophy (Gordon et al., 1967a, 1967b; Penman, 1970; Jaweed et al., 1974). Increases in myofibrillar and sarcoplasmic protein content have been noted after chronic weight lifting (Gordon et al., 1967b; Jaweed et al., 1974), sprint (Wilkinson, 1977) and endurance (Gordon et al., 1967a) activities. Penman (1970) has indicated that increased strength without fiber hypertrophy is associated by alterations in the actin to myosin ratio and an increased contractile element packing density. The second possible mechanism is that of hyperplasia. Both Halls-Craggs (1970) and Reitsma (1970) have shown a longitudinal division of skeletal muscle fibers in response to compensatory overloads. Edgerton (1970) found evidence of an increased hyperplasia in the soleus muscles of rats subjected to a forced swimming protocol. Similar results were not observed in the plantaris or gastrocnemius muscles. Improvements are needed in stimulus quantification and measurement techniques in order to clarify the mechanisms by which skeletal muscle adapts to chronic physical activity overloads.

MOTOR UNIT RECRUITMENT PATTERNS

Selective motor unit recruitment has been shown through glycogen depletion pattern studies with single bouts of exercise (Armstrong et al., 1974, 1977; Gillespie et al., 1974; Sullivan and Armstrong, 1978). Armstrong et al. (1974) and Burke and Edgerton (1975) have identified FOG, SO and finally FG fibers as the preferred sequence of recruitment in rodents for low intensity activity while a FG, FOG and SO pattern exists under high intensity (sprint) conditions. These

recruitment patterns have also been observed in a non-human primate (Gillespie et al., 1974). The work of Gollnick et al., (1973b, 1973c, 1974) suggests a similar recruitment sequence with short duration, high intensity work, but a different pattern (SO, FOG, FG) with endurance activities in humans. This may be related to the smaller size and greater oxidative potential of SO fibers in comparison to FOG fibers in humans. Interestingly, Armstrong et al. (1977) found that the rate of glycogen depletion increased logrithmically with speed in lions, but a large discontinuity in the depletion rate of the three fiber types occurred at the trot-gallop transition. This suggests that quadriceps may exhibit unique nonsequential recruitment patterns with changes in gait. A subsequent investigation by these researchers (Sullivan and Armstrong, 1978) on rats failed to support this suggestion as no gait related glycogen depletion discontinuities were revealed. This data did indicate the existence of a hierarchy of muscle involvement within groups of similarly functioning muscles with a progressively greater utilization of less oxidative fibers located in more peripheral muscles followed by the more peripheral areas of a muscle cross section with increased running speed. These data support the contentions of Maxwell et al. (1973) and Burke and Edgerton (1975) that a specific adaptive response exists within a motor unit which is dependent upon the recruitment pattern associated with the activity. The magnitude of this adaptation is dependent upon the quantity of recruitment of the motor unit.

APPENDIX B

TABLE IV TOTAL DISTANCES RUN DURING CHRONIC PHYSICAL ACTIVITY (CPA) AND A PERFORMANCE TEST BY THE FOUR GROUPS OF ACTIVE ANIMALS

Animal Group and Number	Distance Run (m) CPA	Distance Run (m) Performance Test	Animal Group and Number	Distance Run (m) CPA	Distance Run (m) Performance Test
EAER 16	1960	325	EANA 28	2000	1380
18	1960	417	31	1960	1260
19	1960	199	32	1920	2220
20	2000	220	34	1960	2260
22	1960	311	37	1960	1280
25	1920	329	38	1960	500
Mean	1960	300.2	Mean	1960	1483.3
SEM	10.3	32.6	SEM	10.3	271.7
TAER 39	15120	255	TANA 57	17280	2160
40	16560	278	58	17280	4640
43	16080	479	60	16560	6860
44	17280	806	61	16080	4800
45	17080	1680	63	15120	6980
51	17280	891	67	17080	6960
Mean	16567	731.5	Mean	16567	5400.0
SEM	347.0	218.1	SEM	347.0	785.2

TABLE V INITIAL AND FINAL BODY WEIGHTS FOR THE SIX GROUPS OF ANIMALS

Animal Group and Number	Body Weight (g) 7 Week	Body Weight (g) Sacrifice	Animal Group and Number	Body Weight (g) 7 Week	Body Weight (g) Sacrifice
YCON 1	142	142	CON 3	110	371
2	125	125	5	128	395
4	129	129	8	148	455
6	116	116	9	135	417
11	140	140	10	146	477
12	125	125	13	132	384
Mean	129.5	129.5	Mean	133.2	416.5
SEM	4.0	4.0	SEM	5.6	17.1
EAER 16	132	376	EANA 28	153	357
18	123	397	31	137	435
19	141	397	32	126	361
20	122	390	34	153	370
22	130	364	37	136	360
25	134	393	38	127	357
Mean	133.7	386.2	Mean	138.7	373.3
SEM	4.9	5.5	SEM	4.9	12.5
TAER 39	121	321	TANA 57	145	422
40	156	344	58	132	381
43	128	314	60	141	384
44	154	393	61	144	394
45	146	386	63	114	341
51	149	374	67	160	385
Mean	142.3	355.3	Mean	139.3	384.5
SEM	5.9	13.8	SEM	6.3	10.7

TABLE VI WET WEIGHTS OF THE GASTROCNEMIUS MUSCLE AND ITS RELATIONSHIP TO BODY WEIGHT FOR THE SIX GROUPS OF ANIMALS

Animal Group and Number	Muscle Weight (g)	Relationship[a]	Animal Group and Number	Muscle Weight (g)	Relationship
YCON 1	0.800	5.63	CON 3	1.450	3.91
2	0.532	4.26	5	1.600	4.05
4	0.681	5.28	8	1.689	3.71
6	0.536	4.62	9	1.994	4.78
11	0.648	4.63	10	1.902	3.99
12	0.578	4.62	13	1.590	4.14
Mean	0.629	4.84	Mean	1.704	4.10
SEM	0.04	0.21	SEM	0.08	0.15
EAER 16	1.703	4.53	EANA 28	1.392	3.90
18	1.394	3.51	31	1.511	3.47
19	1.604	4.04	32	1.534	4.25
20	1.482	3.80	34	1.656	4.48
22	1.614	4.43	37	1.612	4.48
25	1.512	3.85	38	1.559	4.37
Mean	1.552	4.03	Mean	1.544	4.16
SEM	0.05	0.16	SEM	0.04	0.16
TAER 39	1.290	4.02	TANA 57	1.630	3.86
40	1.300	3.78	58	1.565	4.11
43	1.254	3.99	60	1.522	3.96
44	1.659	4.22	61	1.510	3.83
45	1.603	4.15	63	1.258	3.69
51	1.618	4.33	67	1.437	3.73
Mean	1.454	4.08	Mean	1.487	3.86
SEM	0.08	0.08	SEM	0.05	0.06

[a] Values represent the ratio "muscle weight x 10^3/body weight".

TABLE VII TOTAL NUMBER OF MUSCLE FIBERS COUNTED PER MUSCLE SAMPLE FOR THE SIX GROUPS OF ANIMALS

Animal Group and Number	No. of Fibers Counted				Animal Group and Number	No. of Fibers Counted			
	VW	VR	SOL	GAST		VW	VR	SOL	GAST
YCON 1	787	728	1155	1066	CON 3	954	758	1095	1029
2	1378	926	985	1083	5	956	546	1735	549
4	1861	1290	1352	1167	8	1407	544	1276	738
6	849	1296	1475	1395	9	1076	544	1024	486
11	1262	684	1101	1363	10	839	552	1394	732
12	1241	893	1212	1416	13	754	662	1273	988
Mean	1230	970	1213	1248	Mean	998	601	1300	754
EAER 16	1259	496	1640	826	EANA 28	939	706	1259	1078
18	898	612	887	1065	31	1739	644	1354	876
19	998	628	1801	1036	32	1022	512	1282	818
20	878	584	1150	875	34	667	670	1263	1026
22	828	620	1296	1066	37	1502	644	1531	747
25	876	624	1465	883	38	1360	648	1310	1252
Mean	956	594	1373	959	Mean	1205	637	1333	966
TAER 39	1008	856	1439	1100	TANA 57	915	542	1533	986
40	574	596	1186	629	58	828	616	1043	681
43	1134	494	1012	1067	60	892	706	1358	756
44	654	560	1176	807	61	855	762	1284	872
45	716	546	1237	959	63	808	548	1077	826
51	605	556	1051	1075	67	644	700	950	893
Mean	782	601	1184	940	Mean	824	646	1208	836

TABLE VIII FIBER TYPE COMPOSITION IN THE VASTUS LATERALIS WHITE MUSCLES OF THE SIX ANIMAL GROUPS

Animal Group and Number	Fiber Types (%)			Animal Group and Number	Fiber Types (%)		
	FOG	FG	SO		FOG	FG	SO
YCON 1	33.4	66.6	0.0	CON 3	6.9	93.1	0.0
2	24.5	75.5	0.0	5	5.7	94.4	0.0
4	32.6	67.4	0.0	8	2.3	97.7	0.0
6	23.4	76.6	0.0	9	1.1	98.9	0.0
11	32.0	68.0	0.0	10	4.7	95.4	0.0
12	23.5	76.5	0.0	13	0.3	99.7	0.0
Mean	28.2	71.8	0.0	Mean	3.5	96.5	0.0
SEM	2.0	2.0		SEM	1.1	1.1	
EAER 16	10.7	89.3	0.0	EANA 28	14.4	85.6	0.0
18	3.8	96.2	0.0	31	12.8	87.2	0.0
19	6.1	93.9	0.0	32	18.5	81.5	0.0
20	12.1	87.9	0.0	34	14.4	85.6	0.0
22	9.2	90.8	0.0	37	14.6	85.4	0.0
25	6.7	93.3	0.0	38	20.5	79.5	0.0
Mean	8.1	91.9	0.0	Mean	15.9	84.1	0.0
SEM	1.3	1.3		SEM	1.2	1.2	
TAER 39	28.4	71.6	0.0	TANA 57	19.6	80.4	0.0
40	24.2	75.8	0.0	58	34.4	65.6	0.0
43	28.0	72.0	0.0	60	31.5	68.5	0.0
44	16.1	83.9	0.0	61	25.6	74.4	0.0
45	28.2	71.8	0.0	63	27.1	72.9	0.0
51	21.8	78.2	0.0	67	29.8	70.2	0.0
Mean	24.4	75.6	0.0	Mean	28.0	72.0	0.0
SEM	2.0	2.0		SEM	2.1	2.1	

TABLE IX FIBER TYPE COMPOSITION IN THE VASTUS LATERALIS RED MUSCLES OF THE SIX ANIMAL GROUPS

Animal Group and Number	Fiber Types (%) FOG	FG	SO	Animal Group and Number	Fiber Types (%) FOG	FG	SO
YCON 1	72.4	22.0	5.7	CON 3	66.5	24.3	9.2
2	72.6	6.9	20.5	5	61.2	38.8	0.0
4	62.5	28.2	9.3	8	61.8	28.7	9.6
6	62.3	6.5	32.3	9	60.3	37.1	2.6
11	73.1	12.3	14.6	10	69.6	16.3	14.1
12	66.2	28.2	5.6	13	66.2	28.7	5.1
Mean	68.2	17.4	14.7	Mean	64.3	29.0	6.8
SEM	2.1	4.1	2.4	SEM	1.5	3.4	2.1
EAER 16	69.0	29.4	1.6	EANA 28	62.6	22.7	14.7
18	66.0	17.3	16.7	31	64.3	30.4	5.3
19	67.5	32.5	0.0	32	53.1	35.6	11.3
20	65.1	27.7	7.2	34	75.5	24.5	0.0
22	63.6	27.4	9.0	37	58.4	36.4	5.3
25	74.7	21.5	3.9	38	67.3	24.4	8.3
Mean	67.6	26.0	6.4	Mean	63.5	29.0	7.5
SEM	1.6	2.3	2.5	SEM	3.1	2.5	2.1
TAER 39	67.5	18.2	14.3	TANA 57	67.5	32.5	0.0
40	77.2	21.8	1.0	58	50.0	49.7	0.3
43	80.2	19.8	0.0	60	63.5	35.7	0.9
44	73.2	14.6	12.1	61	61.7	31.8	6.6
45	66.7	23.8	9.5	63	67.9	32.1	0.0
51	64.8	33.8	1.4	67	63.4	30.3	6.3
Mean	71.6	22.0	6.4	Mean	62.3	35.4	2.3
SEM	2.6	2.7	2.6	SEM	2.7	3.0	1.3

TABLE X FIBER TYPE COMPOSITION IN THE SOLEUS MUSCLES OF THE SIX ANIMAL GROUPS

Animal Group and Number		Fiber Types (%) FOG	FG	SO	Animal Group and Number		Fiber Types (%) FOG	FG	SO
YCON	1	41.7	0.0	58.4	CON	3	4.0	0.0	96.0
	2	31.7	0.0	68.3		5	21.2	0.0	78.9
	4	36.7	0.0	63.3		8	27.0	0.0	73.0
	6	36.5	0.0	63.5		9	0.8	0.0	99.2
	11	38.2	0.0	61.8		10	15.4	0.0	84.6
	12	42.6	0.0	57.4		13	13.4	0.0	86.6
	Mean	37.9	0.0	62.1		Mean	13.6	0.0	86.4
	SEM	1.6		1.6		SEM	4.1		4.1
EAER	16	26.5	0.0	73.5	EANA	28	20.6	0.0	79.4
	18	13.9	0.0	86.1		31	17.5	0.0	82.5
	19	21.4	0.0	78.6		32	15.5	0 0	84.5
	20	10.2	0.0	89.8		34	23.7	0.0	76.3
	22	15.7	0.0	84.3		37	22.3	0.0	77.7
	25	17.7	0.0	82.3		38	11.6	0.0	88.4
	Mean	17.6	0.0	82.4		Mean	18.5	0.0	81.5
	SEM	2.4		2.4		SEM	1.9		1.9
TAER	39	16.3	0.0	83.7	TANA	57	21.6	0.0	78.4
	40	9.6	0.0	90.4		58	22.2	0.0	77.9
	43	16.9	0.0	83.1		60	23.6	0.0	76.4
	44	18.2	0.0	81.8		61	28.7	0.0	71.3
	45	20.8	0.0	79.2		63	17.7	0.0	82.3
	51	10.9	0.0	89.1		67	17.2	0.0	82.8
	Mean	15.5	0.0	84.5		Mean	21.8	0.0	78.2
	SEM	1.8		1.8		SEM	1.7		1.7

TABLE XI FIBER TYPE COMPOSITION IN THE MEDIAL GASTROCNEMIUS MUSCLES OF THE SIX ANIMAL GROUPS

Animal Group and Number	Fiber Types (%) FOG	FG	SO	Animal Group and Number	Fiber Types (%) FOG	FG	SO
YCON 1	55.7	26.2	18.1	CON 3	61.4	21.3	17.3
2	55.1	25.5	19.4	5	59.4	27.5	13.1
4	67.1	17.7	15.2	8	59.2	19.1	21.7
6	63.2	19.3	17.5	9	53.9	23.3	22.8
11	63.2	30.1	6.8	10	56.7	22.5	20.8
12	60.1	24.5	15.4	13	65.1	19.7	15.2
Mean	60.7	23.8	15.4	Mean	59.3	22.2	18.5
SEM	1.9	1.9	1.8	SEM	1.6	1.2	1.6
EAER 16	58.8	22.5	18.6	EANA 28	51.7	24.9	23.5
18	61.0	16.7	22.3	31	50.6	27.1	22.4
19	54.0	22.6	23.5	32	49.0	26.8	24.2
20	53.4	19.8	26.9	34	57.8	28.1	14.1
22	65.1	21.2	13.7	37	55.0	30.5	14.5
25	55.2	18.9	25.9	38	60.3	23.3	16.4
Mean	57.9	20.3	21.8	Mean	54.1	26.8	19.2
SEM	1.9	0.9	2.0	SEM	1.8	1.0	1.9
TAER 39	62.7	17.2	20.1	TANA 57	40.6	36.4	23.0
40	53.4	19.2	27.4	58	40.2	35.1	24.7
43	61.6	17.5	20.9	60	49.2	28.3	22.5
44	63.1	19.6	17.4	61	49.3	35.3	15.4
45	63.3	14.5	22.2	63	45.4	35.7	18.9
51	52.9	23.1	24.0	67	35.3	35.5	29.2
Mean	59.5	18.5	22.0	Mean	43.3	34.4	22.3
SEM	2.0	1.2	1.4	SEM	2.3	1.2	1.9

TABLE XII MEAN FIBER AREAS IN THE MEDIAL GASTROCNEMIUS MUSCLES OF THE SIX ANIMAL GROUPS

Animal Group and Number	[a]Fiber Areas (u^2)			Animal Group and Number	Fiber Areas (u^2)		
	FOG	FG	SO		FOG	FG	SO
YCON 1	857.39	1835.60	1507.22	CON 3	1794.75	2758.39	1717.92
2	1146.57	2455.57	1407.15	5	2179.70	3162.22	2321.58
4	895.90	1669.29	1516.75	8	2089.05	3212.03	2707.45
66	801.68	1311.69	1167.10	9	2408.54	3731.92	2416.37
11	666.90	1334.41	1298.23	10	2065.60	3322.07	2134.68
12	843.90	1084.54	1381.55	13	1937.79	3041.86	2346.45
Mean	868.70	1615.13	1379.65	Mean	2079.21	3204.67	2274.60
SEM	26.87	45.87	31.30	SEM	36.34	50.93	43.63
EAER 16	2023.60	2860.88	2407.42	EANA 28	1670.62	2182.14	1543.90
18	1676.05	2470.50	1680.89	31	1854.24	2356.03	2746.02
19	1500.58	2365.90	1831.70	32	2039.95	3322.94	2668.87
20	2185.44	3412.81	2500.92	34	1510.53	2349.07	1827.83
22	1536.11	2270.68	2041.02	37	1640.54	2609.16	1878.44
25	1084.74	3318.06	2432.91	38	1374.66	2017.07	1787.86
Mean	1833.89	2783.11	2149.12	Mean	1681.73	2472.71	2075.37
SEM	36.43	45.89	39.58	SEM	29.98	46.24	53.44
TAER 39	1815.48	2709.81	1997.77	TANA 57	1688.33	3005.89	2074.70
40	2415.97	3706.17	2735.08	58	2169.88	3625.49	2301.29
43	1733.90	2902.30	2137.75	60	2184.53	3915.05	2428.60
44	2042.32	2972.18	2398.27	61	2091.85	3997.43	2532.81
45	1834.31	2878.04	2217.01	63	2107.36	3562.94	2458.52
51	1836.15	2752.41	2040.55	67	1826.33	3399.64	2218.37
Mean	1946.33	2986.79	2254.38	Mean	2011.36	3584.38	2336.19
SEM	34.71	42.83	36.56	SEM	33.58	53.56	38.37

[a] Values are the means of 30 measurements per fiber type per muscle.

TABLE XIII ESTIMATED PERCENTAGE CONTRIBUTION TO TOTAL MUSCLE AREA (EPTM) OF EACH FIBER TYPE WITHIN THE MEDIAL GASTROCNEMIUS MUSCLES OF THE SIX ANIMAL GROUPS

Animal Group and Number	[a]EPTM (%)			Animal Group and Number	EPTM (%)		
	FOG	FG	SO		FOG	FG	SO
YCON 1	38.8	39.0	22.0	CON 3	55.5	29.6	15.0
2	41.3	40.9	17.8	5	52.4	35.2	12.3
4	53.3	26.3	20.4	8	50.7	25.2	24.1
6	52.6	26.2	21.2	9	47.8	31.9	20.3
11	46.3	44.1	9.6	10	49.6	31.7	18.8
12	51.5	27.0	21.6	13	56.9	27.1	16.1
Mean	47.3	33.9	18.8	Mean	52.1	30.1	17.8
SEM	2.5	3.4	1.9	SEM	1.4	1.5	1.7
EAER 16	52.1	28.2	19.7	EANA 28	48.8	30.7	20.5
18	56.5	22.8	20.7	31	42.8	29.1	28.1
19	45.7	30.1	24.2	32	39.4	35.1	25.5
20	46.4	26.9	26.7	34	48.8	36.8	14.4
22	56.8	27.3	15.9	37	45.8	40.4	13.8
25	47.8	26.1	26.2	38	52.1	29.6	18.4
Mean	50.9	26.9	22.2	Mean	46.3	33.6	20.1
SEM	2.0	1.0	1.7	SEM	1.9	1.9	2.4
TAER 39	56.8	23.2	20.0	TANA 57	30.4	48.5	21.2
40	46.9	25.9	27.2	58	32.2	46.9	20.9
43	52.8	25.2	22.1	60	39.4	40.6	20.0
44	56.3	25.5	18.2	61	36.4	49.8	13.7
45	56.1	20.1	23.8	63	35.5	47.2	17.2
51	46.4	30.3	23.4	67	25.8	48.3	25.9
Mean	52.5	25.0	22.4	Mean	33.3	46.9	19.8
SEM	2.0	1.4	1.3	SEM	2.0	1.3	1.7

[a] Based upon the data in Tables XI and XII.

APPENDIX C

TABLE XIV SUMMARY OF STATISTICAL ANALYSES FOR TOTAL AMOUNT OF CHRONIC PHYSICAL ACTIVITY (CPA)

Analysis of Variance

Source of Variation	SS	MS	DF	F	P
GROUP	1280127700	426708460.00	3	1180.60	≤ 0.001
ERROR	7228672	361433.56	20		

Scheffe Multiple Comparison of Means

Probability Matrix				
	EAER	EANA	TAER	TANA
EAER	-	1.0000	0.0000	0.0000
EANA		-	0.0000	0.0000
TAER			-	1.0000
TANA				-

TABLE XV SUMMARY OF STATISTICAL ANALYSES FOR THE PERFORMANCE TEST

Analysis of Variance

Source of Variation	SS	MS	DF	F	P
GROUPS	97941984	32647328	3	29.45	<0.001
ERROR	22170528	1108526	20		

Scheffe Multiple Comparison of Means

Probability Matrix

	EAER	EANA	TAER	TANA
EAER	-	0.3139	0.9168	0.0000
EANA		-	0.6800	0.0000
TAER			-	0.0000
TANA				-

Scheffe Multiple Means Contrasts

	Contrast	Sch^2	Sig
MODE	END vs SPR	30.89	$p<0.05$
QUANTITY	EX vs TR	17.05	$p<0.05$

TABLE XVI SUMMARY OF STATISTICAL ANALYSIS OF INITIAL BODY WEIGHTS

Analysis of Variance

Source of Variation	SS	MS	DF	F	P
GROUPS	683.69	136.74	5	0.80	0.557
ERROR	5113.88	170.46	30		

TABLE XVII SUMMARY OF STATISTICAL ANALYSES FOR BODY WEIGHTS AT SACRIFICE

Analysis of Variance

Source of Variation	SS	MS	DF	F	P
GROUPS	333692.00	66738.38	5	83.72	<0.001
ERROR	23916.00	797.20	30		

Scheffe Multiple Comparison of Means

Probability Matrix

	YCON	CON	EAER	EANA	TAER	TANA
YCON	-	0.0000	0.0000	0.0000	0.0000	0.0000
CON		-	0.6331	0.2517	0.0336	0.5783
EAER			-	0.9859	0.6167	1.0000
EANA				-	0.9396	0.9925
TAER					-	0.6708
TANA						-

Scheffe Multiple Means Contrasts

Contrast	vs CON	Sch^2	Sig
MODE	END	10.50	N.S.
	SPR	7.09	N.S.
QUANTITY	EX	6.78	N.S.
	TR	10.89	N.S.

TABLE XVIII SUMMARY OF STATISTICAL ANALYSES FOR GASTROCNEMIUS MUSCLE WEIGHTS AT SACRIFICE

Analysis of Variance

Source of Variation	SS	MS	DF	F	P
GROUPS	4.44435	0.89	5	42.17	<0.001
ERROR	.63229	0.02	30		

Scheffe Multiple Comparison of Means

Probability Matrix

	YCON	CON	EAER	EANA	TAER	TANA
YCON	-	0.0000	0.0000	0.0000	0.0000	0.0000
CON		-	0.6539	0.6063	0.1469	0.2736
EAER			-	1.0000	0.9256	0.9873
EANA				-	0.9461	0.9928
TAER					-	0.9995
TANA						-

Scheffe Multiple Means Contrasts

Contrast	vs CON	Sch^2	Sig
MODE	END	8.12	N.S.
	SPR	7.12	N.S.
QUANTITY	EX	4.90	N.S.
	TR	10.92	N.S.

TABLE XIX SUMMARY OF STATISTICAL ANALYSES FOR GASTROCNEMIUS MUSCLE WEIGHTS x 10^3/BODY WEIGHTS

Analysis of Variance

Source of Variation	SS	MS	DF	F	P
GROUPS	3.45825	0.69	5	5.41	0.001
ERROR	3.83667	0.13	30		

Scheffe Multiple Comparison of Means

Probability Matrix						
	YCON	CON	EAER	EANA	TAER	TANA
YCON	-	0.0460	0.0225	0.0829	0.0396	0.0036
CON		-	0.9997	0.9999	1.0000	0.9337
EAER			-	0.9947	0.9999	0.9856
EANA				-	0.9996	0.8392
TAER					-	0.9494
TANA						-

Scheffe Multiple Means Contrasts

Contrast vs YCON		Sch^2	Sig
MODE	END	19.00	$p<0.05$
	SPR	21.16	$p<0.05$
QUANTITY	EX	17.19	$p<0.05$
	TR	23.16	$p<0.05$

TABLE XX SUMMARY OF STATISTICAL ANALYSES FOR FOG FIBER POPULATIONS WITHIN THE VASTUS LATERALIS WHITE MUSCLE

Analysis of Variance

Source of Variation	SS	MS	DF	F	P
GROUPS	3353.51	670.70	5	40.32	<0.001
ERROR	449.02	16.63	30		

Scheffe Multiple Comparison of Means

Probability Matrix

	YCON	CON	EAER	EANA	TAER	TANA
YCON	-	0.0000	0.0000	0.0010	0.7585	1.0000
CON		-	0.5835	0.0010	0.0000	0.0000
EAER			-	0.0834	0.0000	0.0000
EANA				-	0.0426	0.0013
TAER					-	0.8035
TANA						-

Scheffe Multiple Means Contrasts

Contrast vs	YCON	Sch^2	Sig
MODE	END	34.44	p<0.05
	SPR	9.55	N.S.
QUANTITY	EX	63.51	p<0.05
	TR	0.98	N.S.

Contrast vs	CON	Sch^2	Sig
MODE	END	39.20	p<0.05
	SPR	81.73	p<0.05
QUANTITY	EX	17.31	p<0.05
	TR	124.12	p<0.05

TABLE XXI SUMMARY OF STATISTICAL ANALYSES FOR FG FIBER POPULATIONS WITHIN THE VASTUS LATERALIS WHITE MUSCLE

Analysis of Variance

Source of Variation	SS	MS	DF	F	P
GROUPS	3353.38	670.67	5	40.29	<0.001
ERROR	499.38	16.65	30		

Scheffe Multiple Comparision of Means

Probability Matrix

	YCON	CON	EAER	EANA	TAER	TANA
YCON	–	0.0000	0.0000	0.0010	0.7587	1.0000
CON		–	0.5838	0.0010	0.0000	0.0000
EAER			–	0.0836	0.0000	0.0000
EANA				–	0.0427	0.0013
TAER					–	0.8038
TANA						–

Scheffe Multiple Means Contrasts

Contrast vs YCON		Sch^2	Sig
MODE	END	34.40	$p<0.05$
	SPR	9.54	N.S.
QUANTITY	EX	63.44	$p<0.05$
	TR	0.98	N.S.

Contrast vs CON		Sch^2	Sig
MODE	END	39.16	$p<0.05$
	SPR	81.63	$p<0.05$
QUANTITY	EX	17.29	$p<0.05$
	TR	123.98	$p<0.05$

TABLE XXII SUMMARY OF STATISTICAL ANALYSES FOR FG FIBER POPULATIONS WITHIN THE VASTUS LATERALIS RED MUSCLE

Analysis of Variance

Source of Variation	SS	MS	DF	F	P
GROUPS	1169.89	233.98	5	4.20	0.005
ERROR	1670.06	55.67	30		

Scheffe Multiple Comparison of Means

Probability Matrix

	YCON	CON	EAER	EANA	TAER	TANA
YCON	-	0.2326	0.5583	0.2312	0.9450	0.0132
CON		-	0.9917	1.0000	0.7550	0.8192
EAER			-	0.9915	0.9719	0.4642
EANA				-	0.7531	0.8208
TAER					-	0.1203
TANA						-

Scheffe Multiple Means Contrasts

Contrast vs	YCON	Sch^2	Sig
MODE	END	3.16	N.S.
	SPR	15.79	$p<0.05$
QUANTITY	EX	7.38	N.S.
	TR	9.22	N.S.

Contrast vs	CON	Sch^2	Sig
MODE	END	1.80	$p<0.05$
	SPR	0.73	$p<0.05$
QUANTITY	EX	0.16	$p<0.05$
	TR	0.01	$p<0.05$

TABLE XXIII SUMMARY OF STATISTICAL ANALYSIS FOR FOG FIBER POPULATIONS WITHIN THE VASTUS LATERALIS RED MUSCLE

Analysis of Variance

Source of Variation	SS	MS	DF	F	P
GROUPS	365.69	73.14	5	2.24	0.076
ERROR	979.81	32.66	30		

TABLE XXIV SUMMARY OF STATISTICAL ANALYSIS FOR SO FIBER POPULATIONS WITHIN THE VASTUS LATERALIS RED MUSCLE

Analysis of Variance

Source of Variation	SS	MS	DF	F	P
GROUPS	485.37	97.07	5	2.35	0.065
ERROR	1237.56	41.25	30		

TABLE XXV SUMMARY OF STATISTICAL ANALYSES FOR FOG FIBER POPULATIONS WITHIN THE SOLEUS

Analysis of Variance

Source of Variation	SS	MS	DF	F	P
GROUPS	2335.75	467.15	5	13.66	<0.001
ERROR	1025.70	34.19	30		

Scheffe Multiple Comparison of Means

Probability Matrix

	YCON	CON	EAER	EANA	TAER	TANA
YCON	-	0.0000	0.0001	0.0003	0.0000	0.0034
CON		-	0.9239	0.8281	0.9975	0.3399
EAER			-	0.9999	0.9951	0.8973
EANA				-	0.9728	0.9636
TAER					-	0.6170
TANA						-

Scheffe Multiple Means Contrasts

Contrast	vs YCON	Sch^2	Sig
MODE	END	53.54	$p<0.05$
	SPR	36.72	$p<0.05$
QUANTITY	EX	46.10	$p<0.05$
	TR	43.39	$p<0.05$

Contrast	vs CON	Sch^2	Sig
MODE	END	0.98	N.S.
	SPR	5.04	N.S.
QUANTITY	EX	2.30	N.S.
	TR	2.95	N.S.

TABLE XXVI SUMMARY OF STATISTICAL ANALYSES FOR SO FIBER POPULATIONS WITHIN THE SOLEUS

Analysis of Variance

Source of Variation	SS	MS	DF	F	P
GROUPS	2335.63	467.13	5	13.66	<0.001
ERROR	1026.00	34.20	30		

Scheffe Multiple Comparison of Means

Probability Matrix						
	YCON	CON	EAER	EANA	TAER	TANA
YCON	-	0.0000	0.0001	0.0003	0.0000	0.0034
CON		-	0.9239	0.8282	0.9975	0.3401
EAER			-	0.9999	0.9951	0.8974
EANA				-	0.9729	0.9637
TAER					-	0.6172
TANA						-

Scheffe Multiple Means Contrasts

Contrast	vs YCON	Sch^2	Sig
MODE	END	53.52	$p<0.05$
	SPR	36.71	$p<0.05$
QUANTITY	EX	46.08	$p<0.05$
	TR	43.38	$p<0.05$

Contrast	vs CON	Sch^2	Sig
MODE	END	0.98	N.S.
	SPR	5.03	N.S.
QUANTITY	EX	2.30	N.S.
	TR	2.95	N.S.

TABLE XXVII SUMMARY OF STATISTICAL ANALYSES FOR FOG FIBER POPULATIONS WITHIN THE MEDIAL GASTROCNEMIUS

Analysis of Variance

Source of Variation	SS	MS	DF	F	P
GROUPS	1278.25	255.65	5	11.53	<0.001
ERROR	665.19	22.17	30		

Scheffe Multiple Comparison of Means

Probability Matrix

	YCON	CON	EAER	EANA	TAER	TANA
YCON	-	0.9977	0.9536	0.3318	0.9989	0.0001
CON		-	0.9983	0.6021	1.0000	0.0002
EAER			-	0.8441	0.9965	0.0008
EANA				-	0.5593	0.0220
TAER					-	0.0002
TANA						-

Scheffe Multiple Means Contrasts

Contrast	vs YCON	Sch^2	Sig
MODE	END	0.74	N.S.
	SPR	26.13	$p<0.05$
QUANTITY	EX	4.06	N.S.
	TR	15.66	N.S.

Contrast	vs CON	Sch^2	Sig
MODE	END	0.06	N.S.
	SPR	20.21	$p<0.05$
QUANTITY	EX	1.95	N.S.
	TR	11.17	N.S.

TABLE XXVIII SUMMARY OF STATISTICAL ANALYSES FOR FG FIBER POPULATIONS WITHIN THE MEDIAL GASTROCNEMIUS

Analysis of Variance

Source of Variation	SS	MS	DF	F	P
GROUPS	971.14	194.23	5	19.64	<0.001
ERROR	296.68	9.89	30		

Scheffe Multiple Comparison of Means

Probability Matrix

	YCON	CON	EAER	EANA	TAER	TANA
YCON	-	0.9734	0.5677	0.7662	0.1543	0.0003
CON		-	0.9461	0.3084	0.5333	0.0000
EAER			-	0.0479	0.9643	0.0000
EANA				-	0.0056	0.0130
TAER					-	0.0000
TANA						-

Scheffe Multiple Means Contrasts

Contrast vs	YCON	Sch^2	Sig
MODE	END	8.13	N.S.
	SPR	18.16	$p<0.05$
QUANTITY	EX	0.05	N.S.
	TR	2.66	N.S.

Contrast vs	CON	Sch^2	Sig
MODE	END	3.25	N.S.
	SPR	28.20	$p<0.05$
QUANTITY	EX	0.68	N.S.
	TR	7.19	N.S.

TABLE XXIX SUMMARY OF STATISTICAL ANALYSIS FOR SO FIBER POPULATIONS WITHIN THE MEDIAL GASTROCNEMIUS

Analysis of Variance

Source of Variation	SS	MS	DF	F	P
GROUPS	219.16	43.83	5	2.26	0.074
ERROR	580.94	19.36	30		

TABLE XXX SUMMARY OF STATISTICAL ANALYSES FOR FOG FIBER AREAS WITHIN THE MEDIAL GASTROCNEMIUS

Analysis of Variance

Source of Variation	SS	MS	DF	F	P
GROUPS	180468220	36093982.00	5	182.27	<0.001
ERROR	212678660	198024.81	1074		

Scheffe Multiple Comparison of Means

Probability Matrix

	YCON	CON	EAER	EANA	TAER	TANA
YCON	-	0.0000	0.0000	0.0000	0.0000	0.0000
CON		-	0.0001	0.0000	0.1546	0.8375
EAER			-	0.0619	0.3322	0.0142
EANA				-	0.0000	0.0000
TAER					-	0.8606
TANA						-

Scheffe Multiple Means Contrasts

Contrast vs	YCON	Sch^2	Sig
MODE	END	21.07	$p<0.05$
	SPR	19.31	$p<0.05$
QUANTITY	EX	15.97	$p<0.05$
	TR	24.89	$p<0.05$

Contrast vs	CON	Sch^2	Sig
MODE	END	0.72	N.S.
	SPR	1.09	N.S.
QUANTITY	EX	2.09	N.S.
	TR	0.20	N.S.

TABLE XXXI SUMMARY OF STATISTICAL ANALYSES FOR FG FIBER AREAS WITHIN THE MEDIAL GASTROCNEMIUS

Analysis of Variance

Source of Variation	SS	MS	DF	F	P
GROUPS	417845250	83570405.00	5	204.17	<0.001
ERROR	439607300	409317.75	1074		

Scheffe Multiple Comparison of Means

Probability Matrix						
	YCON	CON	EAER	EANA	TAER	TANA
YCON	-	0.0000	0.0000	0.0000	0.0000	0.0000
CON		-	0.0000	0.0000	0.0639	0.0000
EAER			-	0.0009	0.1042	0.0000
EANA				-	0.0000	0.0000
TAER					-	0.0000
TANA						-

Scheffe Multiple Means Contrasts

Contrast vs YCON		Sch^2	Sig
MODE	END	15.76	$p<0.05$
	SPR	19.52	$p<0.05$
QUANTITY	EX	10.02	N.S.
	TR	27.27	$p<0.05$

Contrast vs CON		Sch^2	Sig
MODE	END	1.00	N.S.
	SPR	0.30	N.S.
QUANTITY	EX	3.25	N.S.
	TR	0.06	N.S.

TABLE XXXII SUMMARY OF STATISTICAL ANALYSES FOR SO FIBER AREAS WITHIN THE MEDIAL GASTROCNEMIUS

Analysis of Variance

Source of Variation	SS	MS	DF	F	P
GROUPS	113258500	22652520.00	5	74.66	<0.001
ERROR	325861380	303409.06	1074		

Scheffe Multiple Comparison of Means

Probability Matrix						
	YCON	CON	EAER	EANA	TAER	TANA
YCON	-	0.0000	0.0000	0.0000	0.0000	0.0000
CON		-	0.4589	0.0384	0.9992	0.9502
EAER			-	0.8995	0.6585	0.0653
EANA				-	0.0905	0.0013
TAER					-	0.8521
TANA						-

Scheffe Multiple Means Contrasts

Contrast	vs YCON	Sch^2	Sig
MODE	END	8.91	N.S.
	SPR	9.00	N.S.
QUANTITY	EX	7.08	N.S.
	TR	11.05	$p<0.05$

Contrast	vs CON	Sch^2	Sig
MODE	END	0.07	N.S.
	SPR	0.06	N.S.
QUANTITY	EX	0.35	N.S.
	TR	0.01	N.S.

TABLE XXXIII SUMMARY OF STATISTICAL ANALYSES FOR ESTIMATED PERCENTAGE CONTRIBUTION TO TOTAL MUSCLE AREA (EPTM) OF FOG FIBERS IN THE MEDIAL GASTROCNEMIUS

Analysis of Variance

Source of Variation	SS	MS	DF	F	P
GROUPS	1567.63	313.52	5	13.14	<0.001
ERROR	715.69	23.86	30		

Scheffe Multiple Comparison of Means

Probability Matrix

	YCON	CON	EAER	EANA	TAER	TANA
YCON	-	0.7061	0.8946	0.9997	0.6329	0.0020
CON		-	0.9990	0.5180	1.0000	0.0000
EAER			-	0.7518	0.9963	0.0001
EANA				-	0.4447	0.0048
TAER					-	0.0000
TANA						-

Scheffe Multiple Means Contrasts

Contrast	vs YCON	Sch^2	Sig
MODE	END	3.27	N.S.
	SPR	9.46	N.S.
QUANTITY	EX	0.28	N.S.
	TR	3.23	N.S.

Contrast	vs CON	Sch^2	Sig
MODE	END	0.03	N.S.
	SPR	25.62	$P<0.05$
QUANTITY	EX	2.13	N.S.
	TR	14.31	$P<0.05$

TABLE XXXIV SUMMARY OF STATISTICAL ANALYSES FOR ESTIMATED PERCENTAGE CONTRIBUTION TO TOTAL MUSCLE AREA (EPTM) OF FG FIBERS IN THE MEDIAL GASTROCNEMIUS

Analysis of Variance

Source of Variation	SS	MS	DF	F	P
GROUPS	1818.14	363.63	5	16.73	<0.001
ERROR	652.06	21.74	30		

Scheffe Multiple Comparison of Means

Probability Matrix

	YCON	CON	EAER	EANA	TAER	TANA
YCON	-	0.8451	0.2679	1.0000	0.0829	0.0029
CON		-	0.9181	0.8857	0.6186	0.0001
EAER			-	0.3143	0.9920	0.0000
EANA				-	0.1024	0.0022
TAER					-	0.0000
TANA						-

Scheffe Multiple Means Contrasts

Contrasts vs	YCON	Sch^2	Sig
MODE	END	11.63	N.S.
	SPR	7.39	N.S.
QUANTITY	EX	2.46	N.S.
	TR	0.77	N.S.

Contrasts vs	CON	Sch^2	Sig
MODE	END	3.16	N.S.
	SPR	18.93	$p<0.05$
QUANTITY	EX	0.01	N.S.
	TR	6.30	N.S.

TABLE XXXV SUMMARY OF STATISTICAL ANALYSIS FOR ESTIMATED PERCENTAGE CONTRIBUTION TO TOTAL MUSCLE AREA (EPTM) OF SO FIBERS IN THE MEDIAL GASTROCNEMIUS

Analysis of Variance

Source of Variation	SS	MS	DF	F	P
GROUPS	103.33	20.67	5	1.05	0.407
ERROR	590.43	19.68	30		

APPENDIX D

TABLE XXXVI TRAINING PROGRESSION

Day	Time	Group	Speed m/min	Grade %	Rep	time on min:sec	time off min:sec	Interval[a]	Total on	Total off
1	AM	END	10	5	4	0:30	0:30	-	2:00	2:00
		SPR	10	5	4	0:30	0:30	-	2:00	2:00
2	AM	END	15	10	3	0:30	0:30	-	1:30	1:30
		SPR	15	10	3	0:30	0:30	-	1:30	1:30
3	AM	END	20	15	4	0:30	0:30	-	2:00	2:00
		SPR	20	15	4	0:30	0:30	-	2:00	2:00
6	AM	END	20	15	4	1:00	1:00	-	4:00	4:00
		SPR	30	15	1	1:00	1:00	6	2:30	3:00
7	AM	END	20	15	4	1:30	1:00	-	6:00	4:00
		SPR	40	15	1	1:00	1:00	6	2:30	3:00
9	AM	END	30	15	3	1:30	1:30	-	4:00	4:00
		SPR	60	15	2	0:30	1:30	6	2:30	5:00
	PM	END	30	15	1	1:30	1:30	-	4:00	4:00
		SPR	60	15	2	0:30	1:30	6	2:30	5:00
10	AM	END	30	15	4	1:30	1:00	-	6:00	3:00
		SPR	60	15	3	0:30	1:30	6	3:00	5:00
	PM	END	30	15	4	1:30	1:00	-	6:00	3:00
		SPR	60	15	3	0:30	1:30	6	3:00	5:00
13	AM	END	30	15	1	4:30	-	-	4:30	-
		SPR	60	15	-	-	-	9	2:15	3:00
	PM	END	30	15	1	4:30	-	-	4:30	-
		SPR	60	15	-	-	-	9	2:15	3:00
14	AM	END	40	15	1	3:00	-	-	3:00	-
		SPR	70	15	-	-	-	6	1:30	2:00
	PM	END	40	15	1	3:00	-	-	3:00	-
		SPR	70	15	-	-	-	6	1:30	2:00
16	AM	END	40	15	1	3:00	-	-	3:00	-
		SPR	70	15	-	-	-	9	1:30	3:00
	PM	END	40	15	1	3:00	-	-	3:00	-
		SPR	70	15	1	-	-	9	1:30	3:00
17	AM	END	40	15	1	5:00	-	-	5:00	-
		SPR	80	15	-	-	-	10	2:30	4:30
	PM	END	40	15	1	5:00	-	-	5:00	-
		SPR	80	15	-	-	-	10	2:30	4:30

[a]Intervals of 15 sec. on/30 sec. off.

TABLE XXXVII CHRONIC PHYSICAL ACTIVITY (CPA) REGIMEN

Week	Time	Group	Speed m/min	Grade %	Rep	Interval[a]	Total Time On min.sec.	Total Time Off min.sec.
1,2,3,4	AM	END	40	15	1	-	5:00	-
		SPR	80	15	-	10	2:30	4:30
	PM	END	40	15	1	-	5:00	-
		SPR	80	15	-	10	2:30	4:30
5	AM	END	40	15	1	-	6:00	-
		SPR	80	15	-	12	3:00	5:30
	PM	END	40	15	1	-	5:00	-
		SPR	80	15	-	10	2:30	4:30
6	AM	END	40	15	1	-	6:30	-
		SPR	80	15	-	13	3:15	6:00
	PM	END	40	15	1	-	5:00	-
		SPR	80	15	-	10	2:30	4:30
7	AM	END	40	15	1	-	7:00	-
		SPR	80	15	-	14	3:30	6:30
	PM	END	40	15	1	-	5:00	-
		SPR	80	15	-	10	2:30	4:30
8	AM	END	40	15	1	-	7:30	-
		SPR	80	15	-	15	3:45	7.00
	PM	END	40	15	1	-	5:00	-
		SPR	80	15	-	10	2:30	4:30
9	AM	END	40	15	1	-	8:00	-
		SPR	80	15	-	16	4:00	7:30
	PM	END	40	15	1	-	5:00	-
		SPR	80	15	-	10	2:30	4:30
10	AM	END	40	15	1	-	9:00	-
		SPR	80	15	-	18	4:30	8:30
	PM	END	40	15	1	-	5:00	-
		SPR	80	15	-	10	2:30	4:30

[a]Intervals of 15 sec. on/30 sec. off

APPENDIX E

TABLE XXXVIII COMPARATIVE DATA ON FIBER TYPE COMPOSITION, CROSS SECTIONAL AREA AND ESTIMATED PERCENTAGE CONTRIBUTION TO TOTAL MUSCLE AREA (EPTM) IN THE HETEROGENEOUS GASTROCNEMIUS MUSCLE OF RATS

Author	Year	Animal Age (wk)	CPA Condition	Fiber Types (%)			Fiber Areas (u^2)			EPTM (%)		
				FOG	FG	SO	FOG	FG	SO	FOG	FG	SO
Sullivan and Armstrong[a]	1978	20	Sedentary	54.0	16.0	30.5	3,133	3,729	3,053	52.8	18.6	31.3
Wilkinson[b]	1977	5	Sedentary	59.2	26.3	14.5	808	1,256	1,015	50.0	34.6	15.4
		5	ST (0)[c]	67.1	17.1	15.7	878	1,425	1,067	58.8	24.4	16.7
		15	Sedentary	59.5	21.1	19.4	1,924	2,926	1,844	54.0	29.1	16.9
		15	ST (10)	47.2	36.0	16.8	2,092	3,160	2,137	39.8	44.8	15.5
		25	Sedentary	60.3	18.6	21.1	2,237	3,102	1,945	57.7	24.7	18.6
		25	ST (20)	49.2	33.0	17.8	2,355	3,571	2,258	42.3	43.0	15.7
Sexsmith[b]	1978	7	YCON	60.7	23.8	15.4	869	1,615	1,380	47.3	33.9	18.8
		20	CON	59.3	22.2	18.5	2,079	3,205	2,275	52.1	30.1	17.8
		20	EAER	57.9	20.3	21.8	1,834	2,783	2,149	50.9	26.9	22.2
		20	EANA	54.1	26.8	19.2	1,682	2,473	2,075	46.3	33.6	20.1
		20	TAER	59.5	18.5	22.0	1,946	2,987	2,254	52.5	25.0	22.4
		20	TANA	43.3	34.4	22.3	2,011	3,584	2,336	33.3	46.9	19.8

[a]Used male Sprague-Dawley rats

[b]Used male Wistar rats

[c]Sprint trained for ( ) weeks